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

JON A. FIREHAMMER* AND DENNIS L. SCARNECCHIA

Department of Fish and Wildlife Resources,
University of Idaho, Moscow, Idaho 83844-1136, USA

Abstract.—Paddlefish *Polyodon spathula* of the Yellowstone–Sakakawea stock, Missouri and Yellowstone rivers, Montana and North Dakota, were radio-tagged to assess movement patterns during spawning migrations in 1999–2002. Sixty-three of the 69 tagged fish provided useful data on migratory movements during the study period. Paddlefish exhibited repeated directional changes in movement during the spring, traveling extensively upriver and downriver in association with increasing and decreasing levels of river discharge and suspended sediment. This behavior resulted in their widespread distribution along the lower 50 km of the Yellowstone River during late spring of all 4 years. The choice of river ascended (Missouri or Yellowstone) was also associated with increasing levels of discharge and turbidity. Paddlefish ascended the unregulated Yellowstone River rather than the regulated Missouri River more than four of every five times when moving above the confluence of the two rivers. Although paddlefish were also occasionally contacted in the Missouri River above the confluence, most forays into the Missouri River were of short duration as fish were contacted less than a week afterward in the Yellowstone River. River temperature did not play a significant role in determining directional movement or river selection. The results from this study provide insight into how annual variations in or modifications to the spring flow regime might affect movement patterns in migratory paddlefish and, consequently, spawning success.

The paddlefish *Polyodon spathula*, a large and ancient zooplanktivorous fish, inhabits large-river and reservoir habitats of the Mississippi River system and selected Gulf slope drainages (Russell 1986). Throughout most of their lives, paddlefish feed and overwinter in slow-moving habitats such as backwaters, oxbow lakes, and braided side channels (Stockard 1907; Alexander 1915; Rosen et al. 1982; Hoxmeier and DeVries 1997). In the spring, however, adults undertake extensive upriver migrations to spawning habitats, typically fast-flowing reaches with well-swept gravel bars (Purkett 1961; Pasch et at. 1980) that are often widely separated and distinct from rearing habitats (Rosen et al. 1982). The migrations typically coincide with a specific combination of environmental stimuli including increasing discharge (Pasch et al. 1980; Berg 1981; Paukert and Fisher 2001) and temperature (Purkett 1961; Russell 1986; Lein and DeVries 1998). Long-distance, environmentally cued spawning migrations can be viewed as a strategy to maximize reproductive success in fish (Northcote 1978; Leggett 1985; Dodson 1997). For paddlefish, maintenance of the spawning migration may be important for the persistence of self-sustaining populations (Unkenholz 1986).

To maintain or restore naturally reproducing paddlefish stocks, it is necessary to better understand the influence of river conditions such as discharge, turbidity, and water temperature on spawning migrations. High levels of discharge ensure the inundation and aeration of spawning grounds and may facilitate the downriver transport of larvae to nursery habitats (Russell 1986); consequently, discharge has been considered an important determinant of reproductive success in paddlefish (Wallus 1986; Hesse and Mestl 1993; Hoxmeier and DeVries 1997). In addition, high turbidities associated with the spring freshet most likely decrease the vulnerability of eggs and larvae to predation (Johnson and Hines 1999; Gadomski and Parsley 2005). Low water temperatures may also affect reproductive success by delaying or inhibiting spawning in paddlefish (Pasch et al. 1980; Wallus 1986). However, the influence of discharge, turbidity, and temperature on migratory behavior remains unclear. The lack of upriver movement observed during low-flow years indicates that the magnitude of spring discharge may trigger the spawning migration (Moen et al. 1992; Paukert and Fisher 2001). The duration of high spring flows also has been suggested as an equally im-

* Corresponding author: fire0983@uidaho.edu

Received February 16, 2005; accepted August 4, 2005
Published online December 14, 2005

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.

Study Area

Paddlefish from the Yellowstone–Sakakawea stock rear in Lake Sakakawea, a 156,000-ha Missouri River impoundment in western North Dakota created by the closure of Garrison Dam in 1953. In spring, adults ascend through the reservoir headwaters and into the river in preparation for spawning. Paddlefish have access to about 375 river kilometers (rkm) of the Missouri River from the headwaters of Lake Sakakawea upriver to the tailwaters of Fort Peck Dam, Montana, as well as 114 rkm of the Yellowstone River from its confluence with the Missouri River (hereinafter referred to as the confluence) upriver to the Intake diversion dam (Figure 1). The study area consisted of three reaches: (1) the Yellowstone River (YR), (2) the Missouri River above the confluence (MRAC), and (3) the Missouri River below the confluence (MRBC). Hereinafter, YRkm will refer to river kilometers along the YR, and positive and negative values of MRkm will refer to river kilometers above and below the confluence along the Missouri River, respectively.

The YR has remained mostly unregulated, though a low-head irrigation diversion dam exists at Intake, Montana (YRkm 114). While the dam impedes fish migration, the diverted flow has a negligible effect on the profile of spring discharge (Tews 1994). The YR has thus retained a near-natural hydrograph with increasing flow and sediment load during the spring freshet. Average discharge during May and June at Sidney, Montana (YRkm 47), has been 796 m^3/s, daily average values ranging between 308 and 1,257 m^3/s (water years 1910–2004; USGS 2005). Average suspended sediment during May and June at this station has been 1,741 mg/L for flow years 1972–1976, maximum daily levels attaining 26,800 mg/L. River reaches below Intake are characterized by mul-

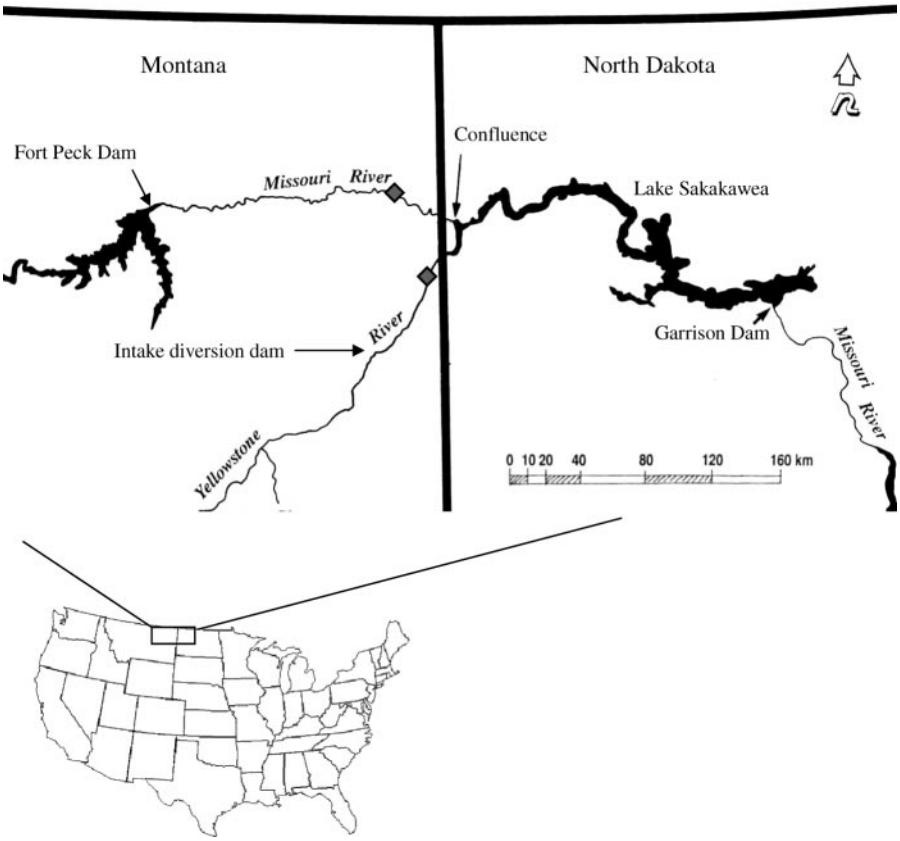

FIGURE 1.—Map of the study area, including the lower Yellowstone River and the Missouri River from Fort Peck Dam to Lake Sakakawea, Montana and North Dakota. The diamonds indicate the U.S. Geological Survey gauging stations at Culbertson (Missouri River river kilometer 63) and Sidney (Yellowstone River 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^3/s, daily average values ranging between 262 and 280 m^3/s (water years 1941–1951, 1958–2004; USGS 2005). Average suspended sediment during May and June at this station has been 612 mg/L for flow years 1972–1976, maximum daily levels attaining only 2,710 mg/L. Temperatures from May to July averaged 8.5°C colder below the dam than in free-flowing reaches above the dam (Gardner and Stewart 1987), though tributary inputs downriver of the dam increased temperatures to more natural levels. Channel gradient in the MRAC ranges between 0.011% and 0.028%, lower than that in the YR (Tews 1994). Although most of the MRAC is characterized by fine sediments with numerous shifting sand bars and was probably entirely depositional before the completion of the dam, gravel and cobble are prevalent in upper reaches due to the erosive nature of sediment-free water released below the dam (Gardner and Stewart 1987).

The MRBC section runs freely for approximately 25–80 rkm, depending on reservoir pool elevation, until it reaches the headwaters of Lake Sakakawea (Scarnecchia et al. 1996). Compared

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

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

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	−0.44
PC-2	30	0.28	0.15	0.89
PC-3	6	−0.29	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:

$$w_i = \frac{\exp(-0.5 \cdot \Delta AIC_c)}{\sum [\exp(-0.5 \cdot \Delta AIC_c)]},$$

where ΔAIC_c was the difference between a given model's AIC_c and the best model's AIC_c (only models with a ΔAIC_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).

The relationship between rate of upriver movement and rate of increasing discharge was assessed by comparing movement rates between different time periods during the spring migration. For 2000, comparisons were drawn between the gradual rise in discharge (187–365 m^3/s) and suspended sediment (74–631 mg/L) that occurred over a 13-d period from April 26 to May 9, and the rapid rise in discharge (163–997 m^3/s) and suspended sediment (75–2,380 mg/L) that occurred over a 13-d period from May 20 to June 2. For 2001, comparisons were drawn between the gradual rise in discharge (150–240 m^3/s) and suspended sediment (59–420 mg/L) that occurred over a 5-d period from May 1 to May 6 and the rapid rise in discharge (200–570 m^3/s) and suspended sediment (70–1,600 mg/L) that occurred over a 5-d period from May 14 to May 19. Only fish that were contacted during both periods within a year were used in the analysis to account for potential differences in movement patterns among fish. Movement rate (km/d) was calculated by dividing movement by number of elapsed days between successive contacts. If more than one movement rate was calculated for a fish during a discharge period, the average of the movement rates was used. To minimize underestimation of movement rates, only movements in which the elapsed period between contacts was less than or equal to 7 d were included in the analysis. Differences in movement rates between discharge periods within a sample year were tested using the Wilcoxon signed rank test (Hollander and Wolfe 1999).

Sex-related differences in movements for 2000 and 2001 were assessed by comparing the cumulative number of river kilometers traversed by males with that of females during the spawning migration. This analysis was only conducted for fish that were still contacted in the river system during June to reduce the variability introduced by fish that were not found throughout the latter part of the migration. A two-factor ANOVA with year and sex as fixed effects was used to test for differences in the distributions of the cumulative river kilometer data.

River selection at the confluence was evaluated by using logistic regression to examine paddlefish responses to the spatial differences in river conditions. This analysis was only conducted for fish that were found above the confluence after a previous contact no more than 3 d earlier below the confluence. As such, only data from the migrations

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	−0.36	−0.19
PC-3	8	0.07	0.31	−0.39

in 2000, 2001, and 2002 were used because of lengthy elapsed periods between contacts for fish during 1999. The selection of either the YR or MRAC was considered the response variable, and the difference in the rate of change in discharge and differences in the magnitude of discharge, turbidity, and temperature between the two rivers were considered as covariates in the analysis. For each movement above the confluence, the difference in the rate of change in discharge was calculated as

$$Q_{Y-M} = (\Delta X_Y - \Delta X_M)/d,$$

where ΔX_Y and ΔX_M are the changes in discharge for the YR and MRAC, respectively (see equation 1), and d is the number of elapsed days between consecutive contacts. A positive Q_{Y-M} indicated that YR discharge was increasing at a greater rate or decreasing at a lesser rate than MRAC discharge, whereas a negative Q_{Y-M} indicated that MRAC discharge was increasing at a greater rate or decreasing at a lesser rate than YR discharge. The difference in the magnitude of discharge, turbidity, and temperature between rivers was calculated for each movement above the confluence as

$$X_{Y-M} = \log_e(X_Y/X_M),$$

where X_Y and X_M are values of the river variable measured above the confluence on the YR and MRAC, respectively. Because the exact date a fish moved above the confluence could not be determined, an average value for X_{Y-M} was calculated for each river variable using the inclusive dates of the elapsed time period between contacts.

As with the directional movement analysis, principal component scores, created to correct for multicollinearity among the original covariates (Table 3), were used as new predictor variables, and model selection methods were used to evaluate the relative plausibility of logistic regression models in predicting river selection. The candidate set comprised models with all possible combinations of the new predictor variables and a model with no predictor variables (i.e., river selection was unrelated to differences between the two rivers). Values for the AIC_c and w_i were used to assess the relative likelihood of each model as best and the relative importance of predictor variables in determining river selection. The logistic discriminant rule derived from the best model was then used to determine the number of observations classified correctly (Johnson 1998).

Results

Telemetry Contacts

Sixty-three of the 69 (91%) tagged paddlefish provided useful migratory data, the number of contacted fish ranging between 20 and 26 during the spring periods of 1999–2002 (Table 4). Six of the 26 fish contacted in 2001 were repeat migrants from the two previous springs, and all fish contacted in 2002 were repeat migrants. Of the repeat migrants, males but not females were contacted in consecutive migrations. A total of 696 contacts were recorded for these 63 fish, the number of contacts ranging between 1 and 23 for individual fish (Table 4). Fish were contacted more frequently

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: Median	Minimum	Maximum	Ascend confluence: 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.

Directional Movements and River Conditions

Migratory movements in 2000 and 2001 were best described by synchronous changes in river discharge and suspended sediment. The first principal component (PC-1), which was strongly and positively correlated with the change in discharge (r = 0.91) and suspended sediment (r = 0.94) (Table 2), was included in the model that best explained directional movement and was the most important regression covariate in the analysis (i.e., it appeared in all models receiving support; Table 5). The positive coefficient estimate for PC-1 indicated that directional movements were positively related to changing levels of discharge and suspended sediment. Ten of 16 (63%) upriver movements greater than 20 km in 2000 occurred during the rapid, concurrent increase in both river variables from May 20 to June 2, whereas only 3 of the 16 (19%) movements occurred during the earlier, more gradual increase in both variables from April 26 to May 9 (Figure 3). Similarly, seven of nine (78%) downriver movements greater than 20 km occurred during intermittent periods of decreasing discharge and suspended sediment from May 9 to May 20 and from June 2 to June 6. In 2001, 22 of 28 (79%) movements greater than 20 km occurred during rapid or prolonged increases in discharge and suspended sediment from May 14 to May 19 and from May 27 to June 6, whereas only 4 of the 28 (14%) movements occurred during the earlier, brief rise in both variables from May 1 to May 5 (Figure 3). Thirteen of nineteen (68%) downriver movements greater than 20 km occurred during intermittent periods of declining discharge and suspended sediment from May 5 to May 14 and May 19 to May 27 in 2001.

The third principal component (PC-3) also contributed to explaining directional movement in both years (relative importance of 0.995; Table 5). This component was weakly but inversely correlated with the change in discharge ($r = -0.29$) and suspended sediment (r = 0.31) (Table 2), and was associated with movement during brief periods when discharge and suspended sediment were not changing in concert. For example, five fish moved more than 20 km upriver during June 1–6, 2001 when YR suspended sediment was increasing rapidly but discharge was relatively stable (Figures 2, 3). In another case, YR suspended sediment decreased during a period of increasing discharge from May 25 to May 31, 2000 (Figure 2). Although two of eleven fish moved more than 20 km upriver during this time, three fish moved only several kilometers upriver and the other six fish moved downriver (Figure 3). The second principal component (PC-2), which was strongly and positively correlated with the change in river temperature (r = 0.89; Table 2), though included in one of the models under consideration as best, was not considered as important as the other two principal components in explaining movement in 2000 and 2001 (relative importance of 0.379; Table 5).

The paddlefish response to changing levels of discharge and suspended sediment resulted in repeated directional changes by individual fish during fluctuating flows in the spring of both years.

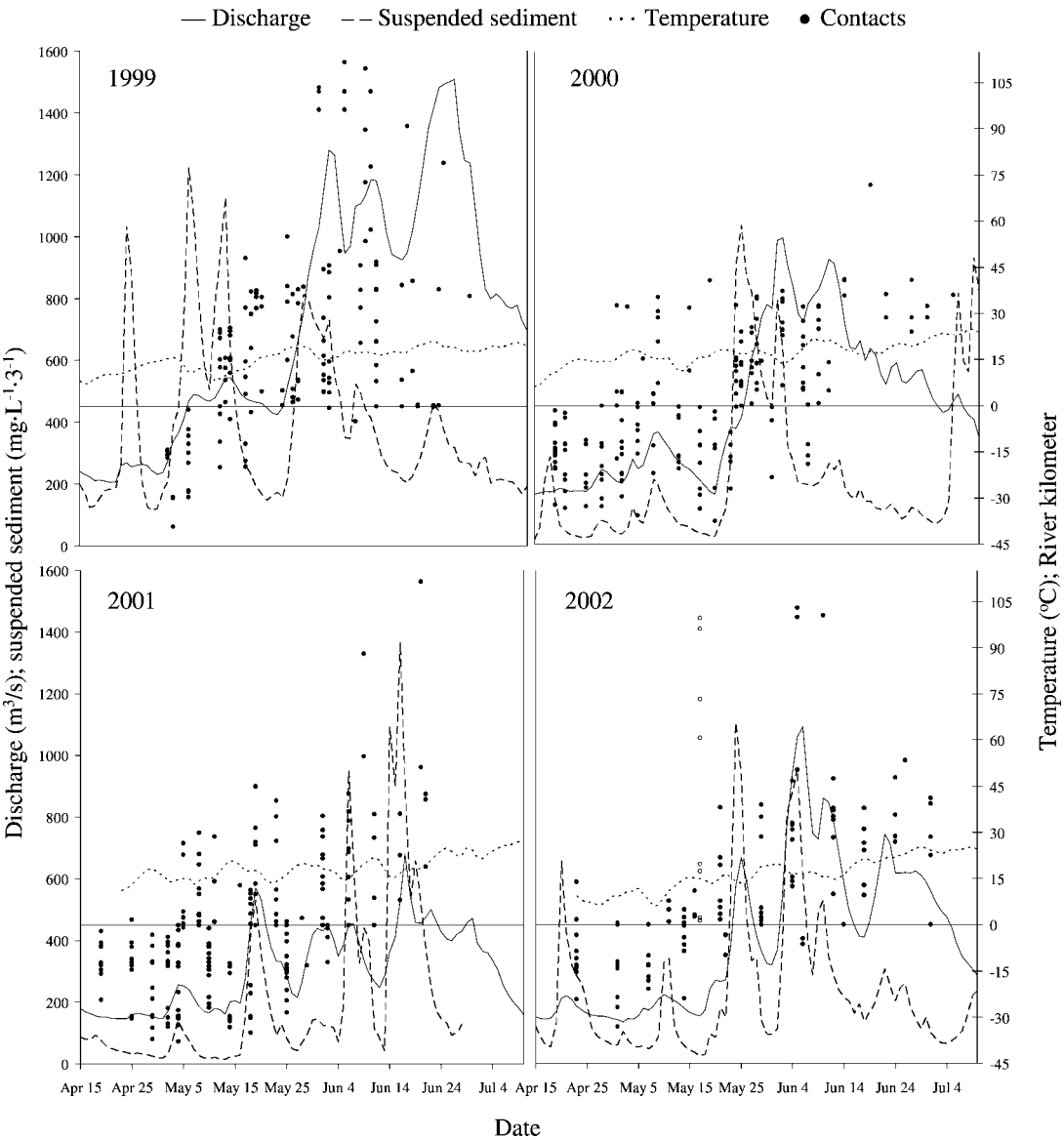

FIGURE 2.—The distribution of radio-tagged paddlefish contacts along the Yellowstone and Missouri rivers in relation to Yellowstone River discharge, suspended sediment, and temperature during migratory periods, 1999–2002. Positive and negative river kilometers (rkm) indicate the number of kilometers 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: $F_{3,21} = 0.3$, $P = 0.82$). 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. Fish did not remain long in the MRAC during any of the 4 years. For 14 of the 17 (82%) fish that were contacted at least once after being contacted along the MRAC, residence time did not exceed 7 d and all were later contacted up the YR. The other three fish, which had been contacted at least 60 rkm up the MRAC in 2002, were later contacted up the YR 12–18 d afterward.

River selection was best predicted by the first principal component (PC-1), which was strongly and positively correlated with the difference in the rate of change in discharge ($r = 0.77$) and the differences in the magnitude of discharge ($r = 0.88$) and turbidity ($r = 0.91$) (Table 3). Not only

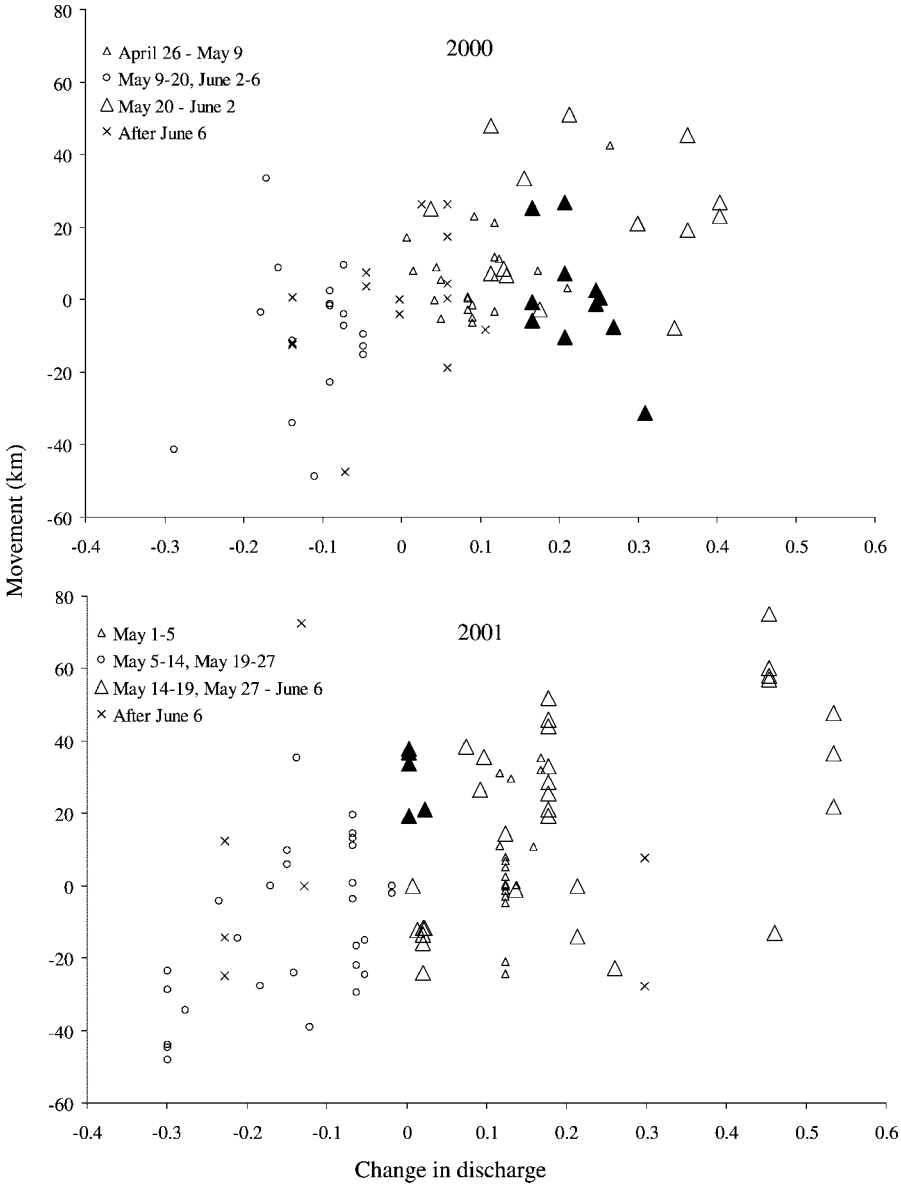

FIGURE 3.—Relationship between movement and the change in discharge (see text for calculation) for migratory radio-tagged paddlefish in the Yellowstone and Missouri rivers, 2000 and 2001. Upriver (positive) and downriver (negative) movements are highlighted during periods of gradually increasing discharge (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 = 1.00, PC-2 = 0.24, PC-3 = 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	−1.9
821	9.2	5.5	−3.7
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	−2.3
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 2.0°C 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. Most of the fish tagged by Zigler et al. (2003) were not sexed or staged and likely included individuals at various stages of development. In fact, the authors captured few gravid females in the navigation pools where tagged fish failed to exhibit coordinated patterns of movement. Although Moen et al. (1992) also tagged fish at various stages of maturation, they noted a lack of synchronized upriver movement within categories of both maturing and mature females. Paddlefish that are not reproductively ready during the spring may not be motivated to migrate and thus may not respond to cues such as increasing discharge.

The degree to which paddlefish migrations were obstructed may have also contributed to the differences in movement patterns observed among studies. Though the Intake diversion dam (YRkm 114) impedes upriver movement on the Yellowstone River, most of the synchronized movements recorded

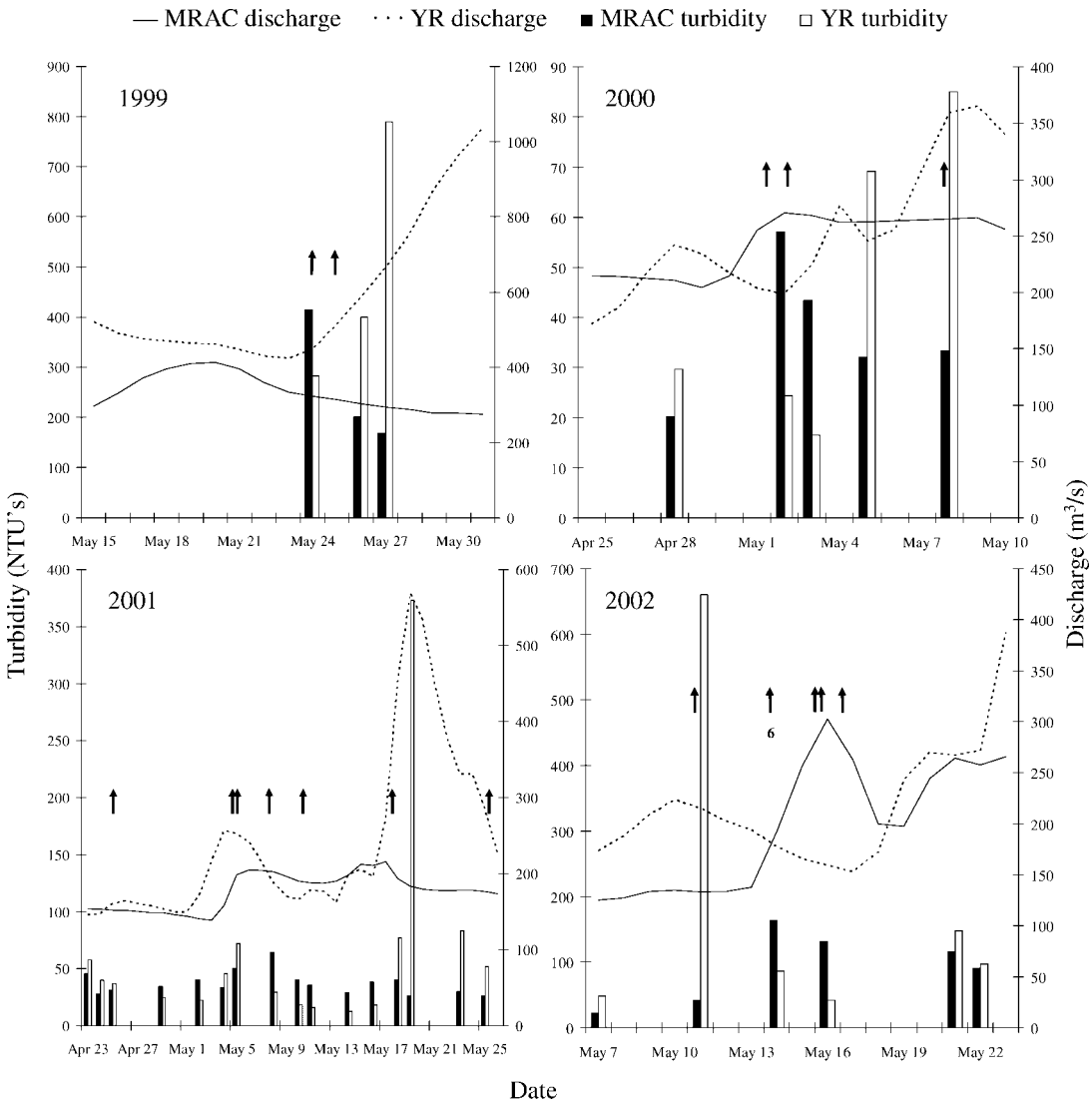

FIGURE 4.—Comparison of discharge and turbidity (nephelometric turbidity units) along the Yellowstone River (YR) and the Missouri River above its confluence with the Yellowstone River (MRAC) during time periods in which radio-tagged paddlefish were contacted along the MRAC, 1999–2002. Arrows indicate 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).

The directional changes associated with changing levels of discharge and suspended sediment demonstrated by paddlefish in this study also do not seem to be a common pattern of behavior found in the phylogenetically related sturgeons *Acipenser* spp., which have many similar life history characteristics as the paddlefish. During the spawning migration, sturgeon typically have been found to make directed upriver movements either to tailwater habitats below dams (Buckley and Kynard 1985; Wooley and Crateau 1985) or to other discrete spawning centers (Hall et al. 1991; Kieffer and Kynard 1993; Foster and Clugston 1997; Paragamian et al. 2002; Heise et al. 2004), and remain there throughout the spawning season. On the other hand, Borkholder et al. (2002) had found migratory lake sturgeon *Acipenser fulvescens* to undergo directional changes in movement, albeit less extensive than in this study, in association with changing levels of spring discharge along the free-flowing Kettle River, Minnesota. Differences in migratory behavior between sturgeon and paddlefish may be a result of their different habitat preferences. Unlike the sturgeon which typically feed on the bottom, the paddlefish, which filter-feed in the water column, may not be as strongly associated with a fixed reference point such as the river bottom. As a result, paddlefish may be more apt to be displaced downriver if periodic decreases in river discharge halt their active upriver movement.

It is unlikely that the repeated directional changes observed in this study represented fractional spawning events for individual fish. In other studies, extensive downriver movements by paddlefish during the spring have typically been associated with the completion of spawning activity (Purkett 1963; Russell 1986). Additionally, paddlefish have been reported to be fractional spawners (Freiberg 1972). However, harvested paddlefish from recreational fisheries along the Yellowstone and Missouri rivers typically reveal no signs of ovulation or spermiation until late May or early June. The repeated downriver movements observed during late April through mid-May were thus more likely a behavioral response during the prespawning migration.

It was difficult to assess the respective influences of suspended sediment and discharge on the paddlefish migration despite our use of principal components to help separate the effects of both river variables. Fish in this study moved upriver as suspended sediment increased amid stable levels of discharge; they also moved downriver as suspended sediment decreased amid increasing levels of discharge. However, evidence was not conclusive as to the contribution of each variable to prespawning movements. Others have suggested that water quality parameters (such as suspended solids) may be important migratory cues for paddlefish (Rehwinkel 1978; Unkenholz 1986). In addition, Gardner and Stewart (1987) observed migratory paddlefish congregating in turbid plumes downriver of tributary mouths along the MRAC. Spawning during high turbidities would likely decrease the vulnerability of deposited eggs and drifting larvae to predation. On the other hand, because suspended sediment and discharge are often highly correlated during the spring, increasing levels of suspended sediment may indicate flow levels that facilitate access to upriver spawning grounds and promote reproductive success. The actual physicochemical constituent on which paddlefish cue during rising discharge, such as current velocity or suspended sediment, remains unclear.

The choice of river that paddlefish ascended was related to differences in the flow regime between the two rivers. Consistent with findings reported by Robinson (1966) and Rehwinkel (1978), the tendency for fish to ascend the YR rather than the MRAC was associated with increasing and higher levels of turbidity and discharge along the less regulated YR. Alternatively, the observed discrepancy in river selection could be attributed to homing tendencies, given the site fidelity that has been posited for migratory paddlefish (Lein and DeVries 1998; Stancill et al. 2002). If natal homing was prevalent in this system, greater reproductive success in the YR could lead to the stronger spawning migration observed in the YR than in the MRAC. Although larval paddlefish have been collected in reaches of the YR and MRAC (Gardner and Stewart 1987; Gardner 1995), a comprehensive assessment of spawning success in both rivers has not been conducted. In addition, prevailing evidence does not support this competing hypothesis. Previous mark–recapture studies conducted in the study area have found individual fish to ascend a given river in one migration and then select the other river in a subsequent migration (Rehwinkel 1978; Frazer 1985). In addition, many of the radio-tagged fish in this study ascended both rivers during the same year. Moreover, ascension up the MRAC typically coincided with brief periods in which turbidity and discharge were higher there than along the YR, corroborating the influence of proximate spatial differences in river conditions on river selection at the confluence. Similarly, Paukert and Fisher (2001) found aspects of

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 14°C 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 10°C. Other studies, in contrast, have found upriver movements to be associated with increasing temperatures above 10°C (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 24°C. Temperatures in excess of 20°C 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 20°C. 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 the context of the migratory mechanisms that have evolved in paddlefish. Many migratory fishes have spawning grounds that are spatially distributed in a sparse but predictable manner and, as a result, have evolved behavioral mechanisms (e.g., piloting and compass orientation) that bias their movement toward the appropriate heading (McKeown 1984; Neill 1984). However, spawning habitat in dynamic large-river environments such as the Yellowstone River may be relatively widespread but unpredictable from year to year, and thus specialized behavior that guides fish toward spatially explicit reaches may not be required. Instead, paddlefish may reach appropriate spawning sites through simple reactive responses (i.e., kineses) to proximate temporal or, in the case of river selection, spatial changes in river conditions during the migration (Harden Jones 1968; Smith 1985; Dodson 1988). Changes in discharge and suspended sediment that stimulate or relax active movement would thus give rise to the patterns of movement observed during this study. In addition, reactive responses that elicit downriver movement to deep pools as discharge recedes may benefit fish by preventing potential stranding in shallow, temporarily dewatered spawning reaches.

The reactive migratory responses exhibited by paddlefish can be further evaluated from the perspective of energetic adaptations. Dodson (1997) postulated that selected migratory traits in iteroparous species of fish should minimize the costs of travel so that energy would be conserved for future reproduction. This postulate runs contrary to the retracing of migratory paths observed in this study. Even female paddlefish, which require a greater energetic investment into reproduction than males (eggs up to 25% of body weight; D. L. Scarnecchia, personal communication), seemingly

behaved inefficiently; their cumulative directional movements during the spawning migration were as great as those of males. Perhaps, as Dodson (1997) speculated, the accumulation of energy reserves prior to migration may serve to counterbalance and perhaps permit inefficient migratory behavior. Such an adaptive tactic may apply in Yellowstone–Sakakawea paddlefish as large quantities of fat surrounding the testes and ovaries have been noted in both mature male and female fish (Scarnecchia, personal communication).

The widespread distribution of paddlefish contacts during the migratory period also suggests that spawning activity was not concentrated in specific sites but widely distributed over the lower Yellowstone River. Although no direct evidence was found that tagged fish spawned, results from this study implied a spatial distribution of spawning grounds that differs from most other studies. Spawning habitat, as confirmed by the collection of eggs or larvae, has usually been identified in tailwater reaches along regulated rivers (Pasch et al. 1980; Wallus 1986; Lein and DeVries 1998). Dams, however, concentrate spawning adults and may have restricted the spatial distribution of spawning activity in these studies. Zigler et al. (2003), on the other hand, found paddlefish distributed over a 106-km reach of the Wisconsin River during the spawning period. Under more natural conditions, the spatial dynamics of large-river environments may favor the distribution of spawning effort over a greater area so that some individuals encounter suitable reproductive conditions (den Boer 1968).

The results from this study indicate that responsive movements by migratory paddlefish to changing levels of spring discharge may affect reproductive success by influencing their spatial distribution in relation to spawning habitat. Brief pulses in fluctuating flow or periods of relatively stable discharge may not sustain active upriver movement and could contribute to the displacement of fish downriver from suitable spawning sites. In addition, more information is needed regarding the components of increasing spring discharge (such as suspended sediment and current velocity) which cue prespawning movements. A clarification of the physicochemical variables to which paddlefish are responding would provide management with a better understanding of the impacts of river modifications on the spawning migration.

Acknowledgments

Funding for this research was provided by the North Dakota Game and Fish Department. We thank G. Power, F. Ryckman, and other staff biologists of the North Dakota Game and Fish Department for their logistical support throughout this project. We are also grateful to S. Shefstad, R. MacKinnon, B. Bowersox, and S. Koerner for their assistance in the field. We also thank anonymous reviewers for their constructive comments on drafts of the manuscript.

References

Alexander, M. L. 1915. More about paddlefish. Transactions of the American Fisheries Society 45:34–39.

Berg, R. K. 1981. Fish populations of the wild and scenic Missouri River, Montana. Montana Department of Fish, Wildlife and Parks, Federal Aid in Fish Restoration, Project FW-3-R, Job 1-A, Helena.

Borkholder, B. D., S. D. Morse, H. T. Weaver, R. A. Hugill, A. T. Linder, L. M. Schwarzkopf, T. E. Perrault, M. J. Zacher, and J. A. Frank. 2002. Evidence of a year-round resident population of lake sturgeon in the Kettle River, Minnesota, based on radiotelemetry and tagging. North American Journal of Fisheries Management 22:888–894.

Bramblett, R. G., and R. G. White. 2001. Habitat use and movements of pallid and shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota. Transactions of the American Fisheries Society 130:1006–1025.

Buckley, J., and B. Kynard. 1985. Yearly movements of shortnose sturgeons in the Connecticut River. Transactions of the American Fisheries Society 114: 813–820.

Burnham, K. P. and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.

Crance, J. H. 1987. Habitat suitability index curves for paddlefish, developed by the Delphi technique. North American Journal of Fisheries Management 7:123–130.

Curtis, G. L., J. S. Ramsey, and D. L. Scarnecchia. 1997. Habitat use and movements of shovelnose sturgeon in Pool 13 of the upper Mississippi River during extreme low-flow conditions. Environmental Biology of Fishes 50:175–182.

den Boer, P. J. 1968. Spreading of risk and stabilization of animal numbers. Acta Biotheoretica 18:165–194.

Dodson, J. J. 1988. The nature and role of learning in the orientation and migratory behavior of fishes. Environmental Biology of Fishes 23:161–182.

Dodson, J. J. 1997. Fish migration: an evolutionary perspective. Pages 10–36 *in* J. J. Godin, editor. Behavioural ecology of teleost fishes. Oxford University Press, Oxford, UK.

Elser, A. A. 1977. Paddlefish investigations. Montana Department of Fish and Game, Federal Aid in Fish Restoration, Project F-30-R-13, Job 2-A, Helena.

Frazer, K. J. 1985. Evaluation of the fishery in the Fort Peck tailwater-dredge cut area and assessment of potential impacts from increased hydropower production at Fort Peck Dam on this fishery. Montana Department of Fish, Wildlife and Parks, Final Report, Helena.

Freiberg, D. V. 1972. Investigation of paddlefish populations in South Dakota and development of management plans. South Dakota Department of Game, Fish, and Parks, Federal Aid in Fish Restoration, Project F-15-R-7, Study 9, Pierre.

Foster, A. M., and J. P. Clugston. 1997. Seasonal migration of Gulf sturgeon in the Suwanee River, Florida. Transactions of the American Fisheries Society 126:302–308.

Gadomski, D. M., and M. J. Parsley. 2005. Effects of turbidity, light level, and cover on predation of white sturgeon larvae by prickly sculpins. Transactions of the American Fisheries Society 134:369–374.

Gardner, W. M. 1995. Yellowstone River paddlefish spawning study. Montana Department of Fish, Wildlife and Parks, Federal Aid in Sport Fish Restoration, Project F-78-R-1, Job 3-E, Helena.

Gardner, W. M., and P. Stewart. 1987. The fishery of the lower Missouri River, Montana. Montana Department of Fish, Wildlife and Parks, Federal Aid in Sport Fish Restoration, Project F-46-R-5, Study 3, Final Report, Helena.

Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. Ecology 84:2809–2815.

Hall, J. W., T. I. J. Smith, and S. D. Lamprecht. 1991. Movements and habitats of shortnose sturgeon, *Acipenser brevirostrum*, in the Savannah River. Copeia 1991:695–702.

Harden Jones, F. R. 1968. Fish migration. Arnold, London.

Heise, R. J., W. T. Slack, S. T. Ross, and M. A. Dugo. 2004. Spawning and associated movement patterns of Gulf sturgeon in the Pascagoula River drainage, Mississippi. Transactions of the American Fisheries Society 133:221–230.

Hesse, L. W., J. C. Schmulbach, J. M. Carr, K. D. Keenlyne, D. G. Unkenholz, J. W. Robinson, and G. E. Mestl. 1989. Missouri River fishery resources in relation to past, present, and future stresses. Canadian Special Publication of Fisheries and Aquatic Sciences 106:352–371.

Hesse, L. W., and G. E. Mestl. 1993. The status of Nebraska fishes in the Missouri River, 1. Paddlefish (Polyodontidae: *Polyodon spathula*). Transactions of the Nebraska Academy of Sciences 20:53–65.

Hollander, M., and D. A. Wolfe. 1999. Nonparametric statistical methods. Wiley, New York.

Hoxmeier, R. J. H., and D. R. DeVries. 1997. Habitat use, diet, and population structure of adult and juvenile paddlefish in the lower Alabama River. Transactions of the American Fisheries Society 126: 288–301.

Johnson, D. E. 1998. Applied multivariate methods for data analysts. Brooks/Cole Publishing, Pacific Grove, California.

Johnson, J. E., and R. T. Hines. 1999. Effect of suspended sediment on vulnerability of young razorback suckers to predation. Transactions of the American Fisheries Society 128:648–655.

Kieffer, M. C., and B. Kynard. 1993. Annual movements of shortnose and Atlantic sturgeons in the Merrimack River, Massachusetts. Transactions of the American Fisheries Society 122:1088–1103.

Koch, R., R. Curry, and M. Weber. 1977. The effect of altered streamflow on the hydrology and geomorphology of the Yellowstone River basin, Montana. Montana Department of Natural Resources and Conservation, Technical Report 2, Helena.

Leggett, W. C. 1985. The role of migration in the life history evolution of fish. Contributions in Marine Science 27:277–295.

Lein, G. M., and D. R. DeVries. 1998. Paddlefish in the Alabama River drainage: population characteristics and the adult spawning migration. Transactions of the American Fisheries Society 127:441–454.

McKeown, B. A. 1984. Fish migration. Timber Press, Portland, Oregon.

Moen, C. T. 1989. Paddlefish movements and habitat use in Pool 13 of the upper Mississippi River during low-water conditions. Master's thesis. Iowa State University, Ames.

Moen, C. T., D. L. Scarnecchia, and J. S. Ramsey. 1992. Paddlefish movements and habitat use in Pool 13 of the upper Mississippi River during abnormally low river stages and discharges. North American Journal of Fisheries Management 12:744–751.

Neill, W. H. 1984. Behavioral enviroregulation's role in fish migration. Pages 61–66 *in* J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill, editors. Mechanisms of migration in fishes. Plenum, New York.

Northcote, T. G. 1978. Migratory strategies and production in freshwater fishes. Pages 326–359 *in* S. D. Gerking, editor. Ecology of freshwater fish production. Wiley, New York.

Northcote, T. G. 1984. Mechanisms of fish migration in rivers. Pages 317–355 *in* J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill, editors. Mechanisms of migration in fishes. Plenum, New York.

Paragamian, V. L., V. D. Wakkinen, and G. Kruse. 2002. Spawning locations and movement of Kootenai River white sturgeon. Journal of Applied Ichthyology 18:608–616.

Pasch, R. W., P. A. Hackney, and J. A. Holbrook II. 1980. Ecology of paddlefish in Old Hickory Reservoir, Tennessee, with emphasis on first-year life history. Transactions of the American Fisheries Society 109:157–167.

Paukert, C. P., and W. L. Fisher. 2001. Spring movements of paddlefish in a prairie reservoir system. Journal of Freshwater Ecology 16:113–124.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. BioScience 47:769–784.

Purkett, C. A., Jr. 1961. Reproduction and early development of the paddlefish. Transactions of the American Fisheries Society 90:125–129.

Purkett, C. A., Jr. 1963. The paddlefish fishery of the Osage River and the Lake of the Ozarks, Missouri. Transactions of the American Fisheries Society 92: 239–244.

Rehwinkel, B. J. 1978. The fishery for paddlefish at Intake, Montana, during 1973 and 1974. Transactions of the American Fisheries Society 107:263–268.

Robinson, J. W. 1966. Observations on the life history, movement, and harvest of the paddlefish, *Polyodon spathula*, in Montana. Proceedings of the Montana Academy of Sciences 26:33–44.

Rosen, R. A., D. C. Hales, and D. G. Unkenholz. 1982. Biology and exploitation of paddlefish in the Missouri River below Gavins Point Dam. Transactions of the American Fisheries Society 111:216–222.

Ross, M. J., and C. F. Kleiner. 1982. Shielded-needle technique for surgically implanting radio frequency transmitters in fish. Progressive Fish-Culturist 44: 41–43.

Ruelle, R., and P. L. Hudson. 1977. Paddlefish (*Polyodon spathula*): growth and food of young of the year and a suggested technique for measuring length. Transactions of the American Fisheries Society 106:609–613.

Russell, T. R. 1986. Biology and life history of the paddlefish: a review. Pages 2–20 *in* J. G. Dillard, L. K. Graham, and T. R. Russell, editors. The paddlefish: status, management, and propagation. American Fisheries Society, North Central Division, Special Publication 7, Bethesda, Maryland.

Scarnecchia, D. L., P. A. Stewart, and G. J. Power. 1996. Age structure of the Yellowstone–Sakakawea paddlefish stock, 1963–1993, in relation to reservoir history. Transactions of the American Fisheries Society 125:291–299.

Smith, R. J. F. 1985. The control of fish migration. Springer-Verlag, Berlin.

Southall, P. D. 1982. Paddlefish movement and habitat use in the upper Mississippi River. Master's thesis. Iowa State University, Ames.

Southall, P. D., and W. A. Hubert. 1984. Habitat use by adult paddlefish in the upper Mississippi River. Transactions of the American Fisheries Society 113: 125–131.

Stancill, W., G. R. Jordan, and C. P. Paukert. 2002. Seasonal migration patterns and site fidelity of adult paddlefish in Lake Francis Case, Missouri River. North American Journal of Fisheries Management 22:815–824.

Stockard, C. R. 1907. Observations on the natural history of *Polyodon spathula*. American Naturalist 41: 753–766.

Tews, A. 1994. Pallid sturgeon and shovelnose sturgeon in the Missouri River from Fort Peck Dam to Lake Sakakawea and in the Yellowstone from intake to its mouth. Montana Department of Fish, Wildlife and Parks, Final Report, Helena.

Unkenholz, D. G. 1986. Effects of dams and other habitat alterations on paddlefish sport fisheries. Pages 54–61 *in* J. G. Dillard, L. K. Graham, and T. R. Russell, editors. The paddlefish: status, management, and propagation. American Fisheries Society, North Central Division, Special Publication 7, Bethesda, Maryland.

USGS (U.S. Geological Survey). 2005. Montana water resource and streamflow data. Available: http://mt.water.usgs.gov/index. (May 2005).

Wallus, R. 1986. Paddlefish reproduction in the Cumberland and Tennessee River systems. Transactions of the American Fisheries Society 115:424–428.

Whalen, K. G., D. L. Parrish, and S. D. McCormick. 1999. Migration timing of Atlantic salmon smolts relative to environmental and physiological factors. Transactions of the American Fisheries Society 128: 289–301.

Winter, J. 1996. Advances in underwater biotelemetry. Pages 555–590 *in* B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Wooley, C. M., and E. J. Crateau. 1985. Movement, microhabitat, exploitation, and management of Gulf of Mexico sturgeon, Apalachicola River, Florida. North American Journal of Fisheries Management 5:590–605.

Zigler, S. J., M. R. Dewey, B. C. Knights, A. L. Runstrom, and M. T. Steingraeber. 2003. Movement and habitat use by radio-tagged paddlefish in the upper Mississippi River and tributaries. North American Journal of Fisheries Management 23:189–205.

Zigler, S. J., M. R. Dewey, B. C. Knights, A. L. Runstrom, and M. T. Steingraeber. 2004. Hydrologic and hydraulic factors affecting passage of paddlefish through dams in the upper Mississippi River. Transactions of the American Fisheries Society 133: 160–172.