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Sex-specific differences in migratory movements of adult paddlefish above Fort Peck Reservoir, Montana, USA

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Abstract. Spring spawning migrations of paddlefish *Polyodon spathula* into the River Missouri above Fort Peck Reservoir, Montana were investigated with radio-telemetry during 2006-2009. Selected migration characteristics (total movement, rate of movement, maximum upriver ascent, duration of the migration, upriver residence time and spawning periodicity) were compared between sexes and among years. Paddlefish exhibited sexual dimorphisms in selected measures of migratory behavior. Females typically moved at a faster rate (mean, 13.4 km/day for females versus 10.1 km/day for males) and remained in the river a shorter time (mean, 40 days) than did males (mean, 45 days). Females and males exhibited similar total movements, upriver residence times and mean maximum ascents. Spawning periodicity was shorter for males (mean, 1.5 years) than females (mean, 2.3 years). Total movement, movement rate, mean duration of the spawning migration and upriver residence time of both sexes differed among years. Results from this study indicate that certain analyses of paddlefish migrations and migratory behavior should be undertaken separately for female and male fish.

Key words: *Polyodon spathula*, migration, sexual dimorphisms, the River Missouri

Introduction

The paddlefish *Polyodon spathula*, a large, migratory zooplanktivore, is distributed throughout large rivers of the Mississippi and Missouri river basins (Vasetskiy 1971, Graham 1997). During the last century, river modifications and over-harvest have reduced abundance and distribution of the species (Gengerke 1986). Channelization, flow regulation, and impoundment have altered feeding habitats, inundated spawning grounds, and impeded spawning migrations (Carlson & Bonislawsky 1981, Sparrowe 1986, Unkenholz 1986). Researchers have long recognized spawning success as a critical and often limiting factor for paddlefish abundance (Russell 1986). In response, numerous studies have investigated the relationships among flow conditions, migratory behavior and reproductive success of the species (Stancill et al. 2002, Firehammer & Scarnecchia 2006, Miller & Scarnecchia 2008).

Paddlefish exhibit a number of sexual dimorphisms. Upon maturation, sexual size dimorphism becomes evident with females in some populations exhibiting average weights 32 % to 57 % greater than males (Purkett 1961, Frieberg 1972, Scarnecchia et al. 1996). The fitness benefits of high egg number (9500-24000 eggs/kg of body weight) of females are largely responsible for weight differences between sexes (Reed et al. 1992, Scarnecchia et al. 2007). Their larger body size and economic value of their eggs have generally made females more targeted by both recreational and commercial harvesters (Scarnecchia et al. 1989, Graham 1997). Reproduction (Peter & Crim 1979) differs between sexes as well with males typically maturing earlier and exhibiting a shorter spawning periodicity than females (Scarnecchia et al. 2007). Given these differences between sexes, sex-specific information on migratory characteristics can provide additional valuable information for sustainably managing paddlefish populations.

Research has indicated that paddlefish require specific environmental conditions such as rising discharges and suspended sediment levels (Firehammer &

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Scarnecchia 2006, Miller & Scarnecchia 2008), and associated changes in water temperature (O'Keefe et al. 2007) to cue upriver movements and to initiate spawning. Successful reproduction of a given population may not only be dependent on the environmental conditions of rivers during the spawning period, but also on the number of migrating female paddlefish that are physiologically prepared to spawn (Scarnecchia et al. 1996, 2007). Therefore, differences in migratory behaviors between sexes need to be clarified for the proper management of the species.

In this paper we examine the migratory movements of telemetered, adult paddlefish in the River Missouri above Fort Peck Reservoir (MRAFP) in central Montana, U.S.A. during four consecutive years (2006-2009). In particular, we investigated differences in migratory behavior between males and females. We hypothesized that, as with many other life-history attributes of paddlefish, rate of movement, total movement, distance of upriver ascent, duration of the migration, upriver residence time and migration periodicity would differ between sexes.

Study Area

The Fort Peck paddlefish stock inhabits the MRAFP between Fort Peck Dam upriver to Morony Dam, 24 km downstream of Great Falls, Montana (Fig. 1). The MRAFP from Morony Dam to the reservoir headwaters is 336 km in length. Two major tributaries enter the river in this reach, the River Marias from the north and the River Judith from the south. Paddlefish are most commonly found in this reach when adults migrate out of the reservoir towards riverine reaches during the spring spawning season (April-July). The MRAFP is characterized by a wide meandering channel, with numerous sand bars, large islands, side channels and back waters. Runoff in the MRAFP typically peaks in June, associated with snowmelt. Mean monthly discharge in the MRAFP at the Virgelle gauging station (USGAS 10040101) over the period 1935 to 2006 has been highest in June (mean, 510 m^3/s) followed by May (mean, 377 m^3/s) and July (mean, 280 m^3/s).

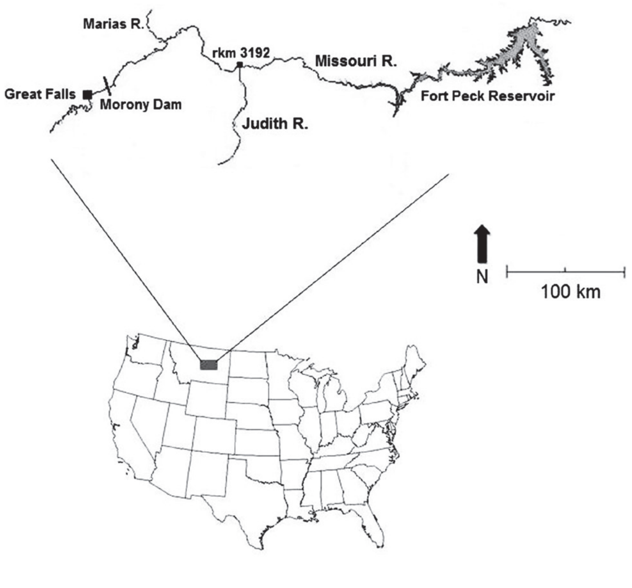

Fig. 1. *Map of the study area including the River Missouri above Fort Peck Reservoir, Montana.*

Material and Methods

Fish capture and tag implantation

Paddlefish migrations into the MRAFP were investigated with radio-telemetry. Drifted, floating gill nets 25 m long by 1.8 m deep (mesh size 12.7 cm) were used to capture mature paddlefish during April and May of 2006-2009. Channel width of sample reaches was approximately 90 m, depths ranged from 1.8 m to 4.5 m and discharge levels ranged from 150 to 490 m^3/s. All capture sites were in the lower zone of the study area between river kilometer (rkm; where numbers refer to kilometers above the River Missouri mouth at St. Louis, Missouri) 3097 and rkm 3034.

One hundred nine fish (65 males and 44 females) were selected for tagging over the four year period (Table 1). In each year, an effort was made to tag equal numbers of males and females. In 2008, high discharge levels decreased gill net capture efficiency and considerably fewer females (3) were able to be tagged than males (16). Males ranged in body length (BL, front of eye to fork of caudal fin; Ruelle & Hudson 1977) from 82.5 cm to 116.8 cm (mean, 95.0 cm) and ranged in weight from 5.7 kg to 24.1 kg (mean, 13.1 kg). Females ranged in BL from 100.3 cm to 134.6 cm (mean, 117.7 cm) and ranged in weight from 18.6 kg to 43.3 kg (mean, 28.3 kg; Table 1).

Lotek Model 3L Microprocessor coded radio transmitters (Lotek Inc. Newmarket, Ontario, Canada) were surgically implanted into each fish. Dimensions of each tag were 16 mm × 73 mm and air-dry mass was 26 gm. Each tag had an estimated battery-life of 4.5 years. Tag implantation surgeries followed the procedure outlined in Firehammer (2004). A 3-4 cm incision was made midway between the pelvic and pectoral fins along the ventral midline of the fish. At this time, sex and maturation stage was determined by observing the gonads through the incision. After tag implantation, the incision was closed with 6-8 non-absorbable sutures. Each surgery took less than five minutes during which time river water was continuously poured across the gills and body to enable the fish to respire and remain moist. After implantation, fish were held in the river and released when swimming movements suggested recovery.

Fixed station and manual tracking

Tracking was conducted using fixed receiving stations and by boat (manual tracking). In 2006, there were four fixed stations on the MRAFP located at rkms 3075, 3088, 3117 and at 3192. In 2007, one more fixed station was installed at rkm 3273. In 2008, a fixed station was added at rkm 3171. In 2009, two more fixed stations were installed, one at rkm 3268, and one at rkm 3337. A 512 kb memory data logger linked to each receiver recorded tag code, signal strength, and time at contact of each passing fish. Fixed station receivers operated 24 hrs/day, seven days a week during the paddlefish migration period (April-July); data were downloaded at bi-weekly intervals.

For manual tracking of paddlefish, an open-bow motorboat was equipped with a Lotek SRX 400 receiver and either a three or four element Yagi antenna (Winter 1996). The MRAFP was divided into three sections for manual tracking: Section 1 from rkm 3000 to rkm 3090, Section 2 from rkm 3091 to 3126, and Section 3 from rkm 3127 to rkm 3192. Manual tracking effort was not divided evenly between sections but was allocated according to discharge levels. During fluctuating flows on the ascending limb of the hydrograph tracking was concentrated on Sections 1 and 2. During the peak of spring discharge tracking was concentrated further upriver on Sections 2 and 3. After peak discharge, tracking was again concentrated downriver on Sections 1 and 2. Each Section was tracked three to five times a week during the appropriate discharge levels.

Once a radio-tagged fish was located, a global positioning unit (GPS) recorded latitude, longitude, and the approximate rkm of each contact site. The United States Geological Survey gauging station near Landusky (station 06115200) recorded mean daily river discharge.

Data analysis

Telemetry contacts were assigned a river kilometer and date to reconstruct the longitudinal distribution of each fish's spring migration. The distance moved between contacts was calculated as the absolute value of the difference between the river kilometer locations of consecutive contacts. Movement rates (km/day) were calculated as the distance moved between consecutive contacts divided by the number of days between contacts. In calculating movement rates, only movements for which the number of days elapsed between contacts were seven days or less were included. Total movement was calculated for each fish as the sum of the distances between all consecutive contacts. In calculating total movement, no restrictions were applied to the number of days elapsed between contacts. However, total movement calculations were limited to fish with at least five observations in a given year. Maximum upriver ascent was defined as the furthest upriver contact of each individual fish. However, contacts from fixed stations that were not operating in all four years were not included in analyses of maximum upriver ascent or total movement. This adjustment allowed the length of the study stretch to be comparable among years. The duration of each individual migration was calculated as the number of days between the first and last telemetry contact for each fish in each year. Upriver residence time was calculated as the proportion of days each individual fish spent above rkm 3088 in relation to their total yearly migration duration. This location was chosen as the boundary between upriver and downriver areas for two reasons. First, this location approximated the upriver extent of most harvest pressure in all four study years. Second, gravels and cobbles (substrates previously shown to be utilized by spawning paddlefish; Purkett 1961,

Table 1. *Mean body lengths and weights of female and male paddlefish* Polyodon spathula *equipped with radio-tags in the River Missouri above Fort Peck Reservoir, Montana in 2006-2009.*

Year	Number of females tagged	Number of males tagged	Mean female body length (cm)	Mean male body length (cm)	Mean female weight (kg)	Mean male weight (kg)
2006	15	15	118.3	99.2	27.5	14.8
2007	14	16	118.0	93.6	27.7	11.7
2008	3	16	116.0	95.4	27.0	13.4
2009	12	18	117.0	97.4	30.3	15.5

Firehammer et al. 2006) are more prevalent above rkm 3088 than below. Migration periodicity was recorded for repeat migrants (fish that migrated in more than one year). We assumed a tag to be stationary if it was repeatedly contacted in the same location with no subsequent movement. Data from stationary tags (assumed to have been shed) were not included in analyses of total movement, maximum upriver ascent, migration duration or periodicity for years during or after tag loss. Daily movement rates were estimated for these tags prior to the time of tag loss.

Preliminary analyses indicated that there was no significant sex/year interaction and that the data were not distributed normally. Therefore the data were rank-transformed and a main effects two-way analysis of variance (ANOVA) was used to test the hypotheses that cumulative distance migrated, mean rate of movement, mean distance of ascent, mean migration duration and mean upriver residence time differed between sexes and among years. In cases in which year was a significant factor, a Student-Newman-Keuls test was used to examine which years differed from one another (Freedman et al. 2007). Differences in the proportions of males and females that exhibited either a one year or two year migration periodicity were examined with a Fisher's exact test (Agresti 1992). Three males tagged in 2006 exhibited consecutive migrations after an alternate year migration. Only the first observation on migration periodicity for these fish was included in analyses. A significance level of 0.05 was used in all hypothesis testing.

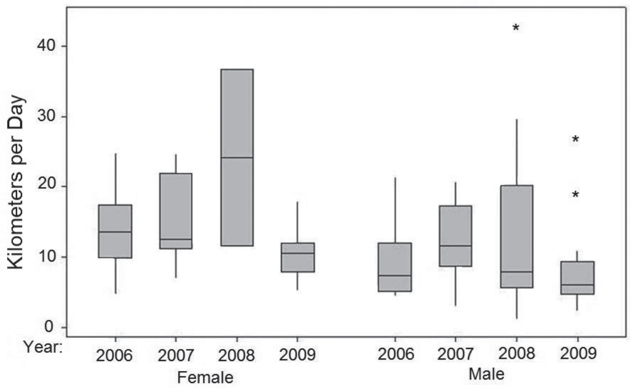

Fig. 2. *Box plots (including median, interquartile range, outliers, and minimum and maximum values) of mean movement rate of female and male paddlefish* Polyodon spathula *in the River Missouri above Fort Peck Reservoir, Montana, 2006-2009.*

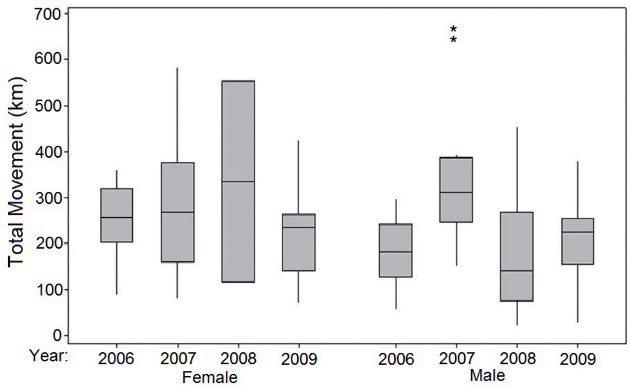

Fig. 4. *Box plots (including median, interquartile range, outliers, and minimum and maximum values) of total movement of female and male paddlefish* Polyodon spathula *in the River Missouri above Fort Peck Reservoir, Montana, 2006-2009.*

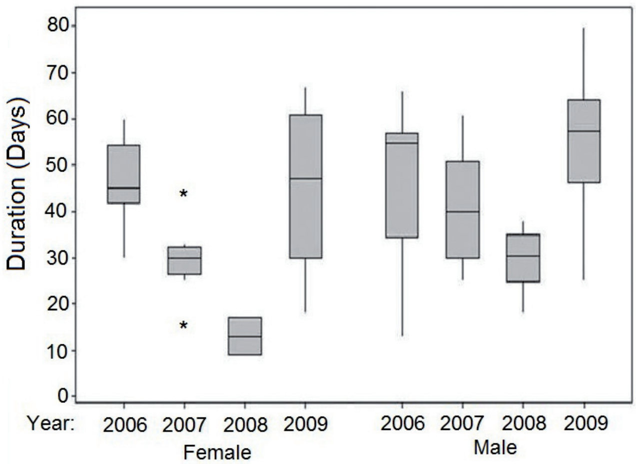

Fig. 3. *Box plots (including median, interquartile range, outliers, and minimum and maximum values) of migration duration of female and male paddlefish* Polyodon spathula *in the River Missouri above Fort Peck Reservoir, Montana, 2006-2009.*

Results

All 109 fish (65 males, 44 females) were subsequently contacted at least once after being equipped with radio tags. Number of contacts for each fish ranged from 1 to 50 contacts (mean, 15.7 contacts/fish/year).

The number of total radio contacts increased with each subsequent year as more tags were implanted (range, 375 in 2006 to 1651 in 2009; mean, 761 contacts). The transmitters of seven females and one male were determined to be stationary during the study period. For these fish, the tags may have been shed or the fish may have died.

Of the 80 fish that were monitored by radio-telemetry in more than one year, 46 were repeat migrants (34 males and 12 females). Males had a significantly shorter migration periodicity (mean, 1.5 years) than females

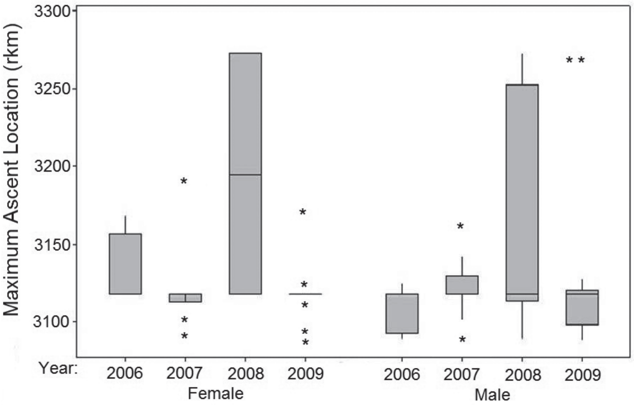

Fig. 5. Box plots (including median, interquartile range, outliers, and minimum and maximum values) of maximum ascent location of female and male paddlefish Polyodon spathula *in the River Missouri above Fort Peck Reservoir, Montana, 2006-2009.*

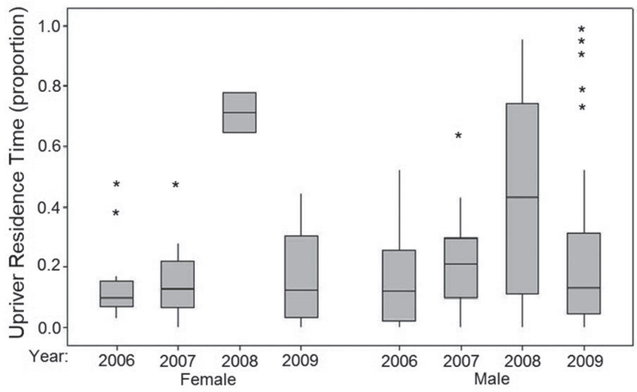

Fig. 6. Box plots (including median, interquartile range, outliers, and minimum and maximum values) of upriver residence time of female and male paddlefish Polyodon spathula *in the River Missouri above Fort Peck Reservoir, Montana, 2006-2009.*

(mean, 2.3 years; Fisher's exact test, P = 0.005). Among males, 17 had a migration periodicity of one year, 16 had a periodicity of two years and one had a periodicity of three years. Among females, none exhibited a migration periodicity of one year, nine had a periodicity of two years and three had a periodicity of three years.

Females typically moved at a faster rate and remained in the river a shorter time than did males (Figs. 2-3). Females moved an average of 13.4 km/day compared to 10.1 km/day for males (ANOVA, F = 19.06, P < 0.01). Males had significantly higher mean migration duration (45 days) than did females (40 days; ANOVA, F = 12.30, P < 0.01). Males spent an average of 28 % of their migration in upriver areas compared to 18 % for females (Fig. 6). However, these differences were not statistically significant (ANOVA, F = 0.37, P = 0.55). Females and males exhibited similar total movements and mean maximum ascents (Figs. 4-5). Females averaged total movement of 248 km per year compared to 220 km per year for males (ANOVA, F = 0.67, P = 0.41). No significant difference was observed for mean maximum ascent between females (rkm 3126) and males (rkm 3128; ANOVA, F = 0.46, P = 0.49). Year played a significant factor in influencing total movement, movement rates, mean duration of the spawning migration and upriver residence time (ANOVA, P < 0.01 for all variables; Table 2) but not mean maximum ascent (ANOVA, F = 0.88, P = 0.45).

***Table 2.** Results of a main effects two-way analysis of variance of migratory movements of radio-tagged female and male paddlefish* Polyodon spathula *in the River Missouri above Fort Peck Reservoir, Montana, 2006-2009.*

Variable	Source of Variation	Degrees of Freedom	Type III Sum of Squares	Mean Square	F-value	P-value
Total Movement	Sex	1	872.4	872.4	0.67	0.41
	Year	3	17465.5	5821.8	4.49	0.005
Movement Rate	Sex	1	20512.1	20512.1	19.06	< 0.0001
	Year	3	22569.9	7523.3	6.99	0.0002
Maximum Ascent	Sex	1	499.7	499.7	0.46	0.49
	Year	3	2860.7	953.6	0.88	0.45
Upriver Residence Time	Sex	1	430.1	430.1	0.37	0.55
	Year	3	15469.2	5156.4	4.38	0.0058
Duration	Sex	1	9765.2	9765.2	12.3	0.0006
	Year	3	67209.5	22403.2	28.21	< 0.0001

Discussion

The lack of sex specific differences in total migration distances observed in our study is a result consistent with other studies. Firehammer & Scarnecchia (2006) found that total movement of migratory paddlefish in the River Yellowstone did not significantly differ between sexes. However, both females (162 km) and males (179 km) had lower mean cumulative distances in their study than in ours (females = 248 km, males = 220 km). Miller & Scarnecchia (2008) also reported no differences in total migration distances between males and females in the River Yellowstone but did identify year as a significant factor influencing total movement. In our study, males were observed to make numerous short range movements whereas females made less numerous but longer range movements. Differences in how travel distances are accumulated should be accounted for when interpreting total movement data of male and female paddlefish.

In our study, female fish moved at a faster rate and exited the river system more quickly after the presumed spawning period than did male fish. Miller & Scarnecchia (2008) also found that males in the River Yellowstone prolonged their migrations. In their study, males were found in spawning reaches up to one month after all radio-tagged females had returned to reservoir habitats. Paragamian & Kruse (2001) found that male white sturgeon *Acipenser transmontanus* in Idaho spent approximately three times longer in spawning reaches than did females. Van Eenennaam et al. (2006) suggested longer residence times at spawning grounds of male green sturgeon *Acipenser medirostris* than females. Hoffnagle & Timmons (1989) found that more males than females from the Lake Kentucky paddlefish stock were found in spawning reaches later in the migration despite a 1 : 1 sex ratio earlier in the migration.

For acipenseriform fishes, these results may be connected to evolutionary differences between sexes in energetic demands for reproduction and in optimal behaviors during the reproduction period. Scarnecchia et al. (2007) presented evidence that the reproductive demands on female paddlefish are greater than for males. Gonadosomatic indices for mature females far exceed those of mature males. Females in northern populations also delay their maturation for several years beyond males associated with increasing their fecundity and energy reserves. Maturing paddlefish accumulate gonadal fat bodies as energy reserves which are depleted with each spawn. Research has shown that these fat reserves are depleted more rapidly in females than males (Scarnecchia et al. 2007). It may thus be more energetically efficient for females to hold in staging areas until environmental cues encourage rapid movement to spawning reaches, rather than making the shorter but more numerous bidirectional movements observed in males. Moreover, a quick return to the reservoir shortly after spawning may benefit females because the increased feeding opportunities may be needed for gonadal recrudescence.

Optimal movement behaviors during reproduction may also differ between sexes. For example, numerous males are believed to accompany one spawning female (Russell 1986), so males can seek out multiple females for spawning opportunities. Under those circumstances, more exploratory (i.e. bidirectional) movements would potentially provide males with fitness benefits not available to females.

Differences in migration periodicity between sexes observed in this study are supported by results of other studies. Long term data from jaw tag returns of Fort Peck paddlefish indicate that spawning periodicity is approximately 50 % every year and 50 % every other year for males and 50 % every other year and 50 % every third year for females (Montana Department of Fish, Wildlife and Parks, unpublished data). In our study, 75 % of female return migrants exhibited an alternate year periodicity and 25 % returned every third year. It is likely that more observations on females with protracted spawning periodicities would have been collected had the study period continued. Differences in spawning periodicities may also be related to sex specific energy demands of reproductive recrudescence. Scarnecchia et al. (2007) found that older fish of the Yellowstone-Sakakawea stock of North Dakota and Montana exhibited less somatic growth and shorter migration periodicities than younger fish. In their study, older males commonly spawned in consecutive years and older females in alternate years. A reliable but non-lethal method of aging old paddlefish has not yet been developed and telemetered fish in our study were not aged. However, age as well as sex data should be incorporated in interpretations of migratory movements when possible.

Migratory paddlefish in this study exhibited sex specific differences in movement rates, migration duration and migration periodicity. These results are in accord with the consistent sex-specific differences documented in many other aspects of paddlefish life history and biology (Scarnecchia et al. 1989, 2007). Although sex may not play a significant factor in influencing all migratory movements, results from this study and past studies of sex differences indicate that analyzing paddlefish migrations and migratory behavior should be undertaken separately for female and male fish.

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