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ORIGINAL PAPER

The influence of discharge on duration, ascent distance, and fidelity of the spawning migration for paddlefish of the Yellowstone-Sakakawea stock, Montana and North Dakota, USA

Jon A. Firehammer · Dennis L. Scarnecchia

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Abstract Paddlefish, *Polyodon spathula*, of the Yellowstone-Sakakawea stock, Missouri and Yellowstone Rivers, Montana and North Dakota, were radio-tagged to assess the influence of spring discharge on duration of river residency, ascent distance, and site-fidelity during spawning migrations of 1999–2002. Contrary to expectations and reported results from other paddlefish populations, fish remained in the river for similar periods of time and ascended to similar reaches in years of higher, more sustained discharge and in years of lower, more fluctuating discharge. In all years, 65 of the 74 migrants (88%) restricted their ascent to reaches below Yellowstone River kilometer (YRkm) 55; only six migrants were found to further ascend to upriver reaches within 20 river kilometers (rkm) of the Intake Diversion Dam (YRkm 114). The lack of detectable annual differences in ascent distance over the study period despite annual differences in Yellowstone River spring flow regimes may have been partially attributed to the apparent site-fidelity demonstrated by the tagged fish over the study period. Ten of the 22 paddlefish contacted in more than one spring migration repeatedly limited their upriver movement to sites that were within 10 rkm of each other. In addition, similar to the reproductive homing tendencies documented in other large-river migratory fishes, site-fidelity occurred in different reaches of the river system. Results from this study suggest that, in years of moderate discharge, site-fidelity may be as influential as the spring flow regime in determining the reaches to which migratory paddlefish ascend. Further research is needed to investigate potential differential spawning success in fish that return to different reaches of the lower Yellowstone River.

Keywords *Polyodon spathula* · Yellowstone River · Reproductive homing · Radio-telemetry

Introduction

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). Paddlefish predominantly forage and overwinter in low-velocity habitats such as backwaters, oxbow lakes, and braided side-channels (Rosen et al. 1982; Hoxmeier and DeVries 1997). In spring, however, adults undergo extensive upriver migrations, coincident with periods of increasing discharge and temperature (Purkett 1961; Pasch et al. 1980; Lein and DeVries 1998;

J. A. Firehammer (✉) · D. L. Scarnecchia
Department of Fish and Wildlife Resources,
University of Idaho, Moscow, ID 83844-1136, USA
e-mail: drjfirehammer@hotmail.com

Paukert and Fisher 2001), to access spawning habitat, typically fast-flowing reaches with well-swept gravel bars (Purkett 1961; Pasch et al. 1980). In several populations, spawning success (Wallus 1986; Hesse and Mestl 1993) and year-class strength (Hoxmeier and DeVries 1997; Paukert and Fisher 2001) have been associated with years of high sustained spring discharge. Proposed mechanisms by which sustained, high flows may contribute to successful reproduction include the increased flushing of fine sediments from spawning substrate, the ensured inundation of incubation sites, and the more successful transport of emerging larvae to suitable off-channel nursery grounds (Russell 1986).

Aspects of the spring flow regime may also affect reproductive success in paddlefish by influencing both the duration and ascent distance of the adult spawning migration. The spawning migration may be aborted in years of fluctuating, low spring discharge if motivational cues are suspended. Low flows may also fail to stimulate persistent upriver movement resulting in the distribution of migrants downriver from suitable spawning habitat. Studies have found a lack of upriver movement from downriver rearing areas and an absence of paddlefish at upriver spawning sites in years of fluctuating, low spring discharge compared to ascension to suitable spawning sites in years of higher flows (Purkett 1961; Paukert and Fisher 2001). Rapid decreases in spring discharge have also been noted to precipitate the abandonment of spawning reaches in the white sturgeon, a phylogenetically related species (Paragamian and Kruse 2001).

Site-fidelity, however, may also influence the spatial distribution of migrants along spawning reaches irrespective of inter-annual differences in the spring flow regime. Although homing is most often associated with salmonids (Dittman and Quinn 1996), site-fidelity has been demonstrated for other large-river fishes that undergo extensive riverine migrations. Adults from paddlefish (Lein and DeVries 1998; Stancill et al. 2002; Zigler et al. 2003) as well as Gulf sturgeon, *Acipenser oxyrinchus desotoi* (Wooley and Crateau 1985; Foster and Clugston 1997; Heise et al. 2004), Colorado pikeminnow, *Ptychocheilus lucius* (Tyus 1990; Irving and Modde 2000), and razorback sucker, *Xyrauchen texanus* (Tyus and Karp 1990; Modde and Irving 1998) populations have been found to return to sites attended to in previous migrations.

Many paddlefish populations have limited potential to provide insight into the mechanisms influencing the duration and distance of the spawning migration because their movement patterns have been altered by large river modifications. River regulation curbs the rise in spring discharge, suppressing migratory cues (Moen et al. 1992), and dams concentrate adults in tailwater habitats, impeding their upriver movement (Southall and Hubert 1984; Zigler et al. 2004). In contrast, investigations conducted along a more unregulated river system would afford a better opportunity to further assess the relative effects of annual spring discharge and site-fidelity on migratory tendencies in paddlefish.

The Yellowstone-Sakakawea paddlefish stock is one of the last naturally-reproducing populations in the United States, and has persisted as a result of access to suitable, spawning habitat in the lower Yellowstone River (Scarnecchia et al. 1996). The Yellowstone River, which has no large main-stem impoundments, has retained much of the natural variability in discharge that has been considered important for successful paddlefish reproduction. A radio telemetry study was conducted during 1999–2002 to assess the influence of annual differences in the Yellowstone River flow regime on the duration and distance of the spawning migration. It was hypothesized that fish would remain in spawning reaches longer and migrate further up the Yellowstone River in years of high, sustained spring discharge than in years of low, fluctuating spring discharge. In addition, the telemetry study permitted multi-year observations of individual migrants to examine potential site-fidelity in staging and reproductive habitats within the river system.

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 (MR) from the headwaters of Lake Sakakawea upriver to the tailwaters of Fort Peck Dam, Montana, as well as 114 rkm of the Yellowstone River (YR) from its confluence with the MR (hereinafter referred to as the Confluence) upriver to the Intake Diversion Dam (Fig. 1). Paddlefish have been found to typically ascend the YR rather than the MR during their spawning migration (Robinson 1966; Rehwinkel 1978).

The YR and MR exhibit vastly different flow regimes during the spring. Flow dynamics along the MR above the Confluence have been highly altered since the completion of Fort Peck Dam in 1937 (Hesse et al. 1989). As a result of flow stabilization, average MR discharge during May and June at Culbertson, Montana [Missouri River km (MRkm) 63] for water years 1941–1951 and 1958–2004 has been 273 $m^3\ s^{-1}$, with daily averages ranging between 262 and 280 $m^3\ s^{-1}$ (USGS 2005).[1] In contrast, the YR has remained mostly unregulated, though two low-head irrigation diversion dams exist at Intake [Yellowstone River km (YRkm) 114] and Cartersville (YRkm 382) in Montana. Although dams impede 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 elevated levels of discharge during spring. Average discharge during May and June at Sidney, Montana (YRkm 47) for water years 1941–2004 has been 755 $m^3\ s^{-1}$, with daily averages ranging between 311 and 1143 $m^3\ s^{-1}$ (USGS 2005).

Habitat characteristics differ among reaches of the lower YR accessible to migratory paddlefish (Bramblett and White 2001). River reaches below the Intake Diversion Dam contain multiple islands and alluvial channel bars. Current is swift and substrate consists primarily of cobble and gravel, substrate types considered most suitable for paddlefish spawning and egg incubation (Crance 1987). Along the lowermost 45 rkm of the YR islands and channel bars remain common, although sand replaces cobble and gravel as the predominant substrate. In addition, sand is the most common substrate type of the MR below the Confluence.

Methods

Field procedures

We captured paddlefish in reaches below the Confluence by drifting modified gill nets (mesh sizes 7.6, 10.2, and 12.7 cm) perpendicular to the channel current. Upon contact with nets, fish were removed and brought on board the boat where length (eye-to-fork length (EFL); Ruelle and Hudson 1977) and weight were recorded, and sex noted during surgical implantation of transmitters (Ross and Kleiner 1982). We implanted radio transmitters into 69 adult paddlefish 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. 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 (lengths 97–109 cm EFL (mean, 103 cm), each weighing 20.9 kg) could not be determined. Mean lengths and weights were not significantly different among the three tagging groups for either females or males (ANOVA; $P > 0.1$). Although we did not determine maturation stage 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.

Radio transmitters (Advanced Telemetry Systems, Isanti, MN) used in this study each had a unique frequency between 49.011 and 49.930 Mhz, and a life expectancy of 1100 days which enabled fish to be monitored over several years. We implanted transmitters of three different dimensions

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[1] USGS (US Geological Survey). 2005. Montana water resource and streamflow data homepage. http://mt.water.usgs.gov/index.

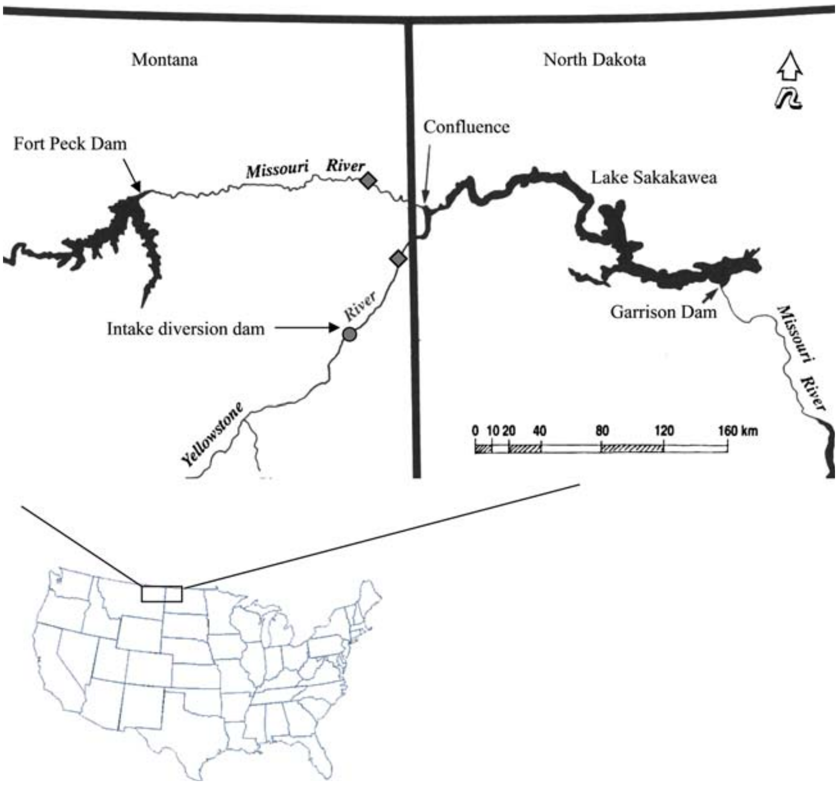

Fig. 1 Map of the study area including the lower Yellowstone River and the Missouri River from Fort Peck Dam to Lake Sakakawea, Montana and North Dakota. The filled circle represents the Intake diversion dam (Yellowstone River river kilometer 114), and the filled diamonds indicate the US Geological Survey gauging stations at Culbertson (Missouri River river kilometer 63) and Sidney (Yellowstone River river kilometer 47), Montana

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).

We divided the study area into three manageable units that were surveyed primarily by boat using a directional loop antenna: (1) YRkm 114–YRkm 47; (2) YRkm 47–Confluence; and (3) a 40 km stretch extending downriver from the Confluence. Aerial surveys were conducted periodically, particularly along the MR above the Confluence due to its poor accessibility by boat. We surveyed the three study units weekly during the spring to determine the presence and location of individual fish along the river system. Geographical coordinates were recorded for all contacted fish using a global positioning system receiver and later overlaid onto a digitized map of the river system using geographic information systems software (ARC/INFO, Environmental Systems Research Institute, Inc., Redlands, California). During spring surveys, a tag that had been consecutively contacted in the same location along the river for a period longer than 30 days was assumed to have been expelled. Tracking was not conducted during the summer after fish were no longer contacted in the river (indicating their probable return to Lake Sakakawea) because the radio transmitters were not easily detected at reservoir depths. During the fall and winter, we conducted surveys below the Confluence to identify staging areas occupied by fish that would participate in the forthcoming spring migration; fish were surveyed only 1–4 times per month during this time because of lack of movement. We monitored river conditions during the study by obtaining daily YR discharge (m^3 s^{-1}) from the United States Geological Survey (USGS) gauging station near Sidney, Montana (YRkm 47), and daily temperatures from a data logger positioned at YRkm 13.5.

Data analyses

We assessed the influence of the flow regime on the duration of the spawning migration by examining the dates at which individual fish were last contacted during the spring. The date of last contact, or exit time, for an individual fish was considered to represent either the premature termination of the migration, or a close approximation to spawning time as paddlefish have been found to move quickly back downriver after spawning (Russell 1986). Because the entire study area was not surveyed every day and survey dates differed among years, we assigned exit times to weekly periods to minimize bias when assessing differences among years. Ten weekly periods were delineated, the first period starting on May 1 and the last period ending on July 9. We qualitatively examined distributions of exit times for all 4 years by plotting Kaplan–Meier curves, which depicted the proportion of fish remaining in the river throughout annual survey periods (Allison 1995).

Event-time analysis, which has recently been used in fisheries research to model passage rates at dams (Castro-Santos and Haro 2003; Zigler et al. 2004; Naughton et al. 2005), permitted a closer examination of inter-annual differences in the weekly number of paddlefish exiting the river system (i.e., weekly exit rates). We employed a Cox proportional hazards regression (PHREG) model to explore the effects of the spring flow regime on weekly exit rates across survey years:

$$h_{i(t)} = \lambda_0(t)\exp[\beta_1 x_{i1} + \cdots + \beta_k x_{ik}(t)]$$

where $h_{i(t)}$ is the probability (hazard) of an individual fish i exiting the river system at week t given that the individual has not yet exited. The model structure relates individual probabilities to an unspecified baseline function, $\lambda_0(t)$, and to a set of predictor covariates x_{i1},..., x_{ik}, the effects of which are estimated by the coefficients β_1,..., β_k. The PHREG model has several advantageous features for describing the type of data collected in this study (Allison 1995; Castro-Santos and Haro 2003). Briefly, time-dependent covariates could be incorporated into the model allowing exit probabilities to change during annual survey periods. In addition, individuals that were present at the beginning of a survey but not found to exit could still be included in the analysis as part of the “at large group” until considered censored. Fish were considered censored when they (i) were harvested, (ii) no longer moved upriver but were contacted in the same location suggesting tag expulsion, or (iii) were still present in the river during the final survey week, which differed among years. We included year effects as categorical covariates in the model to assess gross annual differences in exit rates; a significant year effect for a given survey year would indicate that fish exited more quickly in any given week in that year versus other years. Because spawning events, and hence exit times, may be triggered by peaking levels of spring discharge (Purkett 1961; Wallus 1986; Lein and DeVries 1998), annual differences in exit rates within a given week may be attributed to annual differences in the timing of peak discharge events. To represent these finer-scale differences in annual flow patterns, we included a time-dependent covariate in the model which calculated the change in YR discharge during the preceding week. A significant positive (negative) effect for this covariate would indicate that fish exited more quickly in any given week in years where the preceding week’s discharge had been increasing (decreasing) compared to years where the preceding week’s discharge had been decreasing (increasing). PHREG modeling was performed using SAS v.8 (SAS Institute Inc., Cary, NC) with the exact option for breaking ties (Allison 1995).

We evaluated annual differences in the ascent distance of the spawning migration using ANOVA. The furthest rkm contact up the YR represented the migratory extent for an individual fish.

If a fish was not found to ascend the YR, it was assigned a negative value representing the number of rkm below the Confluence where it was contacted. We excluded fish from the analysis that were harvested, had presumably expelled their tags, or ascended the MR above the Confluence and thus not subjected to levels of YR discharge. Because non-normality was detected in the residuals, data were log-transformed after adding a scaling factor to every rkm to eliminate negative values. In addition to year, we initially included sex as a factor in the ANOVA model but found it to be insignificant (sex: $F = 0.08$, df = 1, $P = 0.78$; sex*year interaction: $F = 1.10$, df = 3, $P = 0.36$) and eliminated it from further analyses to include fish of unknown sex. Bartlett's test of equal variances was also performed on the data to examine annual differences in the dispersion of furthest contact rkm (Neter et al. 1990).

We used linear regression to examine fidelity to potential spawning reaches for fish that participated in two migrations. Furthest upriver contacts from subsequent migrations were regressed on furthest upriver contacts from initial migrations while setting the intercept parameter to zero. An estimated slope parameter that was not significantly different from unity would indicate that individual fish migrated to similar reaches in different years. In other words, fish that had migrated far up the YR were likely to return to distant sites up the YR, whereas fish that had limited their migration to YR reaches near the Confluence were likely to return to these same downriver sites. We assessed fidelity to particular staging areas by qualitatively examining the relative distribution of contacts in reaches below the Confluence during fall and winter survey periods.

Results

The annual profiles of the YR spring flow regime exhibited both similarities and differences among study years (Fig. 2). Generally, the longest periods of increasing discharge occurred from late May to early June in all 4 years. However, fluctuations in YR discharge were less prevalent in 1999 and 2000 than in 2001. During 1999 and 2000, discharge increased for periods of at least 10 days, whereas periods of continuously rising discharge lasted no longer than 6 days during 2001. Peak discharge during the study was much higher in 1999 ($1509\ \mathrm{m}^3\ \mathrm{s}^{-1}$) than in 2001 ($680\ \mathrm{m}^3\ \mathrm{s}^{-1}$) with intermediate levels recorded in 2000 ($997\ \mathrm{m}^3\ \mathrm{s}^{-1}$) and 2002 ($1093\ \mathrm{m}^3\ \mathrm{s}^{-1}$). However, all 4 years exhibited peak flows below the median YR peak flow recorded over the last 50 years. Maximum spring discharge in 1999–2002 represented the 49th, 18th, 2nd, and 33rd percentiles, respectively.

We contacted 62 of the 69 (90%) radio-tagged paddlefish during the study, the number of contacted fish ranging between 19 and 26 in spring survey periods of 1999–2002. Twenty-five fish (17 males, 7 females, and 1 fish of unknown sex) were contacted in at least two of the four spring migrations with 3 of these 25 contacted in three different migrations. Females were contacted every 2 or 3 years, and males were typically contacted every other year or in successive years; the seven males contacted in consecutive migrations were all contacted in 2001 and 2002. A total of 695 contacts was recorded, the number of contacts ranging between 1 and 23 for individual fish. We contacted fish more frequently in 2000 (median, 10.5 contacts) and 2001 (median, 8.5 contacts) than in 1999 (median, 4 contacts) and 2002 (median, 4.5 contacts). In 1999 and 2000, we did not contact paddlefish in repeat surveys during July, suggesting their return to the reservoir by this time; five fish were still present in the river system in each of 2001 and 2002 during final surveys conducted on June 21 and July 1, respectively. We concluded that six of the 62 fish expelled their transmitters during their spring upriver migrations. In addition, five males and one female were harvested in North Dakota and Montana sport fisheries during the study.

Radio-tagged paddlefish generally remained in the river system for similar periods in all 4 years. Few fish exited early in each spring; 91, 74, 76, and 86% of the fish were still contacted in the river system on May 29 in 1999–2002 (Fig. 3). In addition, many fish exited during June in all 4 years in association with peak periods of YR discharge and river temperatures in excess of 13°C (Fig. 2). Ninety-one, 61, 51, and 58% of the

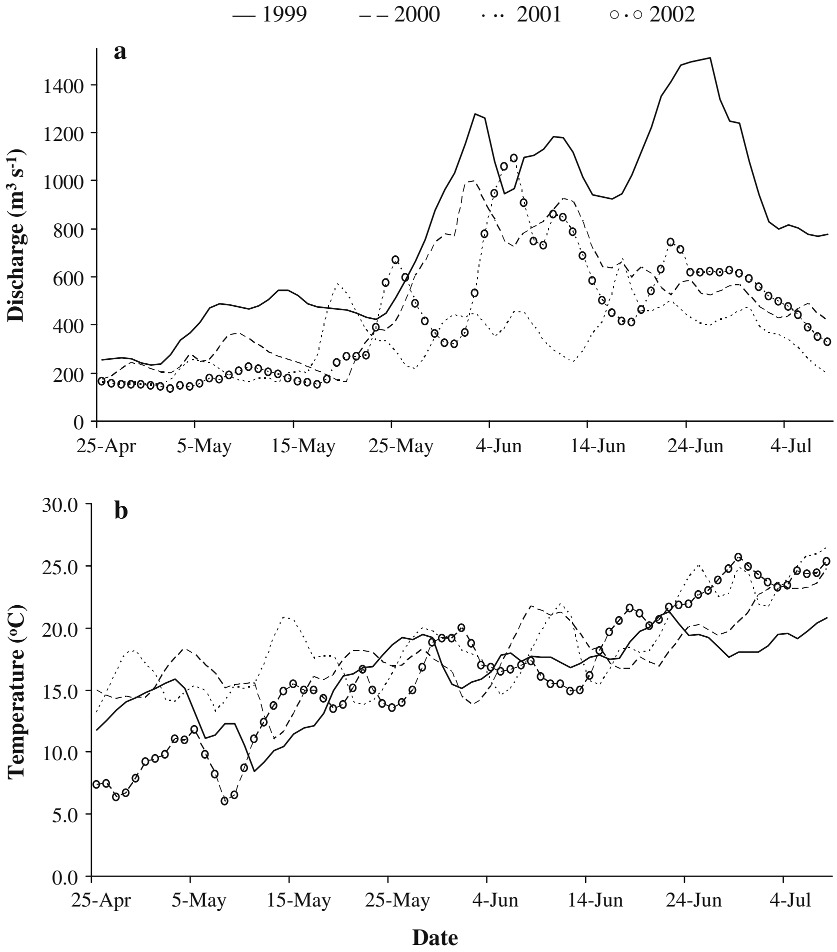

Fig. 2 Daily lower Yellowstone River discharge (**a**) and temperature (**b**) during spring migratory periods, 1999–2002

fish were last contacted during June in 1999–2002 (Fig. 3). Results from the PHREG model corroborated the lack of detectable annual differences in migration duration. The rates at which fish exited in any given week were not significantly different among years over the survey weeks (PHREG, Likelihood ratio = 1.086, df = 3, $P = 0.78$).

We detected fine-scale differences in exit patterns, however, when annual differences in the profile of June discharge were accentuated by the inclusion of the time-dependent discharge covariate in the PHREG model. During particular weeks in June, significantly more fish were found to exit in years where the preceding week's discharge had been decreasing than in years where the preceding week's discharge had been increasing (PHREG, Likelihood ratio = 12.12, df = 1, $P = 0.0005$, discharge covariate coefficient = –0.0025). For example, seven fish in each of 1999 (38%) and 2000 (47%), compared with only one (5%) fish in 2002, were last contacted during June 5–11 (Fig. 3). Whereas YR discharge had been declining after a peak on June 2 in both 1999 and 2000, discharge was rapidly increasing during the week prior to June 5 in 2002 (Fig. 2). Peaks in discharge occurred both earlier (May 25) and later (June 6) in 2002 concurrent with periods of last contact for nine (47%) of the migrants during May 29–June 4 and June 12–18 in that year (Fig. 3). Incidentally, the effect of the weekly discharge pattern was not significant when data from 2002 were removed from the PHREG analysis.

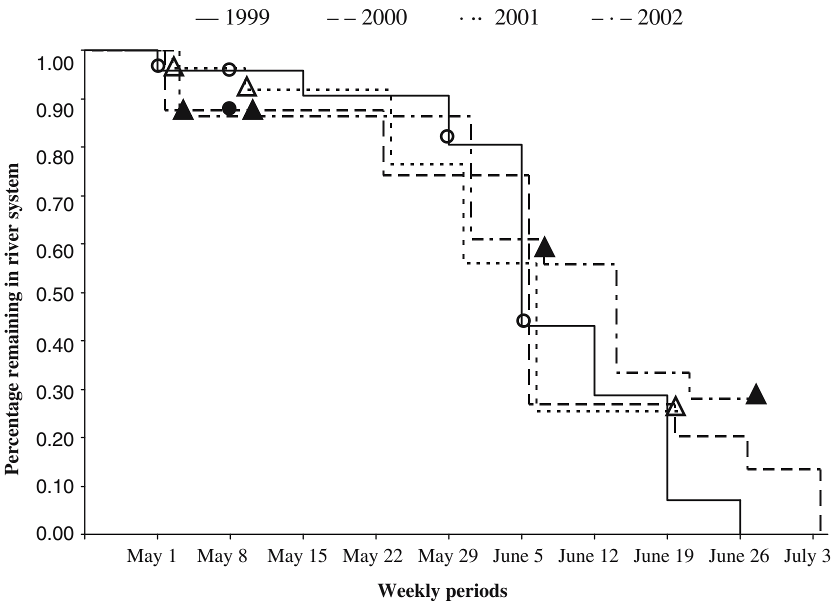

Fig. 3 Kaplan–Meier curves depicting residence times of radio-tagged migratory paddlefish in the Yellowstone and Missouri rivers, 1999–2002. Individual exit dates were grouped into weekly periods. Open (1999) and filled (2000) circles and open (2001) and filled (2002) triangles indicate weeks where fish were censored during the four springs. Note that curves for each year are staggered to provide clarity for comparison

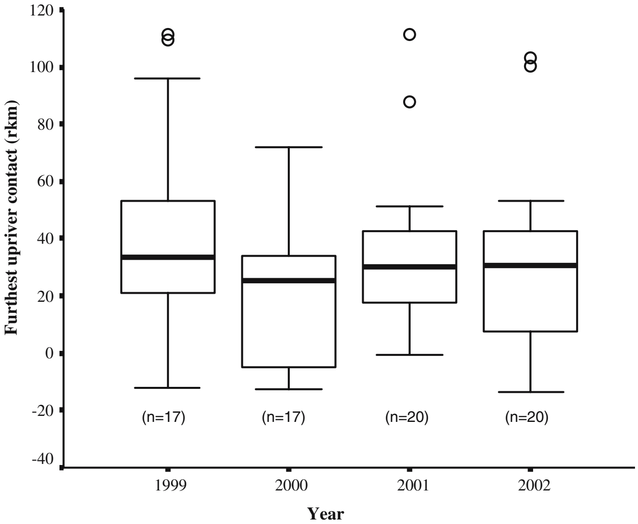

Fig. 4 Distribution of furthest upriver contacts (rkm) for radio-tagged paddlefish during migratory periods, 1999–2002. Positive values indicate distance up the YR and negative values indicate distance below the Confluence. The dark bars within boxes represent medians, and the box lengths represent the interquartile ranges. The whiskers indicate the distance to the largest and smallest observed values that are <1.5 box lengths from either end of the box, and the open circles represent observed values that are between 1.5 and 3.0 box lengths from either end of the box. Sample sizes are provided in parentheses

Year did not have a significant effect on either the mean (ANOVA, $F = 2.12$, df = 3, $P = 0.106$) or dispersion (Bartlett's test, $\chi^2 = 1.53$, df = 3, $P = 0.68$) of furthest upriver contacts for migratory paddlefish. In both high and low flow years, many of the fish limited their ascent to the lower

55 rkm of the YR (Fig. 4); 65 of the 74 (88%) migrants that provided useful data on ascent distance were not contacted further upriver than YRkm 55. In addition, 11 of the furthest upriver contacts were below the Confluence; 9 of these 11 fish were not contacted after the first week in May, and 7 of these 9 fish were males. We contacted four fish further upriver than YRkm 55 during the high flow year of 1999; we contacted two fish within this reach during the low flow year of 2001. Only six migrants were contacted within 20 rkm of the Intake Diversion dam (YRkm 114) during the study.

Furthest upriver contacts for repeat migrants were comparable in successive migrations suggesting fidelity to particular reaches during migratory periods. For 10 of the 22 (45%) paddlefish, furthest upriver contacts were within 10 rkm of each other in repeat migrations; 3 of these 10 fish returned to the same respective reaches of the YR in three of the four springs (Fig. 5). In addition, some fish moved only short distances upriver in successive migrations, whereas others consistently returned to reaches far up the YR (Linear regression, $R^2 = 0.69$, 95% confidence interval for slope parameter = $0.578 \leq \beta \leq 1.088$). For example, five fish were never contacted further than YRkm 13.5, whereas seven fish repeatedly returned to the same river reach between YRkm 28 and 53 (Fig. 5). In contrast, we contacted one fish further upriver than YRkm 100.0 in 3 of the 4 years including both the high-flow year of 1999 and the low-flow year of 2001 (Fig. 5). During fall and winter survey periods, fish occupied specific staging reaches below the Confluence (Fig. 6). Eighty-nine, 69, and 80% of the contacts were concentrated within a reach 12–15 rkm below the Confluence in 1999, 2000, and 2001, respectively. An additional reach 33–36 rkm below the Confluence accounted for 11% of contacts in 2000 and 12% of contacts in 2001. We consistently contacted 22 of the 25 (88%) repeat migrants in these particular staging areas.

Discussion

The lack of annual differences in migratory duration and ascent distance for paddlefish

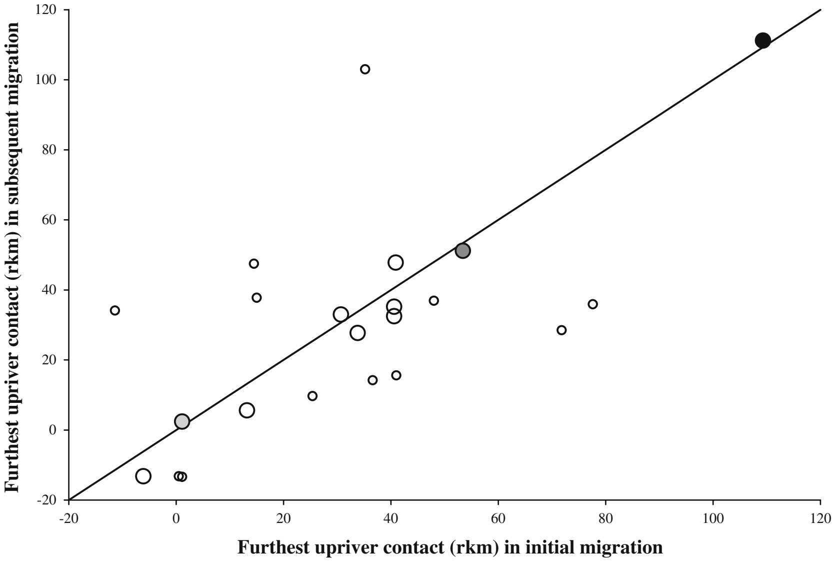

Fig. 5 Furthest upriver river kilometers (rkm) recorded for radio-tagged paddlefish contacted in more than one migration, 1999–2002 (reference line of unity slope indicates equivalent distances in subsequent migrations). Positive values indicate distance up the YR and negative values indicate distance below the Confluence. Enlarged circles represent fish that were contacted at sites within 10 rkm of each other. Filled circles of black, dark grey, and light grey represent three fish that were contacted at YRkm 100, 53, and 10 in their third migrations, respectively (Note that for each of these fish the rkm attained in the third migration was comparable to the rkm attained in the first two migrations as expressed by the point on the graph)

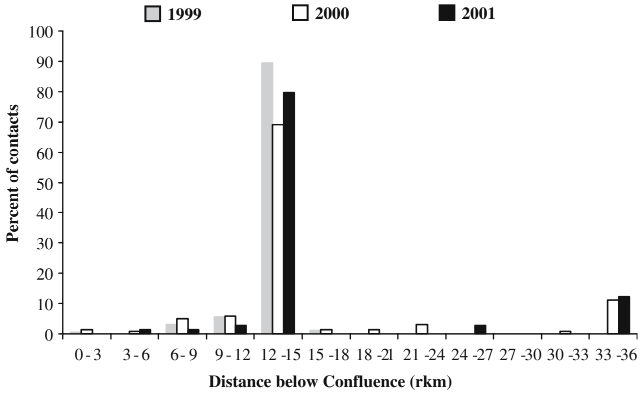

Fig. 6 The percent of radio-tagged paddlefish contacts distributed among partitioned 3-km reaches below the Confluence during fall and winter survey periods, 1999–2001

despite annual differences in YR spring flow regimes is not consistent with what is expected based on the results of other paddlefish studies that have detected a positive relationship between discharge and ascent distance. In a multi-year study in Oklahoma, Paukert and Fisher (2001) found fish to ascend to upriver reaches of the Arkansas and Salt Fork Rivers in a year in which spring discharge exceeded 1500 $m^3 s^{-1}$, but did not find fish to leave downriver staging reaches in a year in which discharge was more stable and did not exceed 52 $m^3 s^{-1}$. Similarly, Purkett (1961) observed many paddlefish at upriver spawning sites along the Osage River, Missouri in years with extended periods of high spring discharge, but observed few fish upriver in a year of few and rapidly subsiding spring rises. Compared with these studies, the lack of a detectable relationship in our study could be attributed to the degree of difference in flow regimes among years. Although peak YR discharge in 2001 (680 $m^3 s^{-1}$) was less than half that in 1999 (1509 $m^3 s^{-1}$), the magnitude of difference was much smaller than that observed in the study by Paukert and Fisher (2001). In addition, although paddlefish have been found to display repeated directional changes in movement in association with fluctuating spring discharge (Firehammer and Scarnecchia 2006), the intermittent 6-day flow pulses in 2001 were evidently of sufficient magnitude and duration to sustain migratory activity and provide adequate depths for movement to reaches similar to those frequented by migrants in other higher flow years. Compared to the variation in YR spring flows over the last 50 years, the range in discharge recorded during 1999–2002 was only moderate, with peak flows below the median value. Under higher flow conditions, the distribution of migratory paddlefish along YR reaches may differ markedly from that observed in our study.

Although analyses did not reveal gross annual differences in migratory tendencies over the study period, intra-seasonal patterns in the duration and distance of the migration were detected. In each spring, several fish, mostly males, were last contacted in early May and limited their ascent to reaches below the Confluence. The reason for their early departure and abbreviated ascent is unknown. These fish may have spawned early, may have prematurely terminated their spawning migration, or may have been incapable of spawning that year. Whatever the reason, the lack of upriver movement displayed by these fish was consistent with that observed in both immature and mature but non-gravid paddlefish in other research (Filipek 1990). Though gonadal samples collected from male paddlefish harvested in Montana and North Dakota recreational fisheries have indicated that over 95% are capable of spawning in the spring (authors, unpublished data), the maturation stage of radio-tagged males in this study was not assessed. In contrast to the low numbers of these early-exiting fish, many adults in each year remained in the river longer and were last contacted in June, exiting the river after YR flows had crested. Departure times for these fish, as approximations to spawning dates, suggests a triggering of reproductive activity associated with peak river discharge, a relationship similar to that found in other paddlefish populations (Purkett 1961; Wallus 1986; Lein and DeVries 1998).

The lack of contacted fish in reaches below the Intake Diversion Dam, especially in the higher flow year of 1999, was also unexpected given the disparity in the number of paddlefish harvested at Intake (a good indication of fish abundance) in different flow years. Whereas only 360 fish were harvested in the recreational fishery during the low flow year of 2001, 1706 paddlefish were taken by fishermen during the high flow year of 1999. The apparent incongruity between the catch and telemetry data may be attributed to one or more of several factors from our study, including the discrepancy in contact frequency among years, the effects of tag implantation on movement patterns, and the tagging of a non-random sample of migratory adults. Because fish were contacted less frequently in 1999 than in other years and have been found to exhibit rapid changes in directional movement (Firehammer and Scarnecchia 2006), fish may have been temporarily present below Intake in 1999 but not contacted during survey periods. In addition, fish that had migrated in 1999 were tagged in late April immediately prior to the initial rise in YR discharge. At the time of release, any stress incurred during the surgery could have suppressed the upriver response to increasing flow. Unexpected downriver movements have been observed in sturgeon studies after excessive handling during tagging procedures (Hall et al. 1991; Moser and Ross 1995). Alternatively, radio-tagged fish may not have been a representative sample of the migratory segment of the population. Fish chosen for tagging were biased toward those that displayed fidelity to particular staging reaches below the Confluence. Other staging sites not targeted in this study may have harbored paddlefish that had different migratory tendencies. Associations between overwintering reaches used by staging fish and ascent distances in the following spring migration have been documented in sturgeon populations (Bemis and Kynard 1997; Kynard 1997).

Many of the repeat migrants in this study limited their upriver movement to the same river reaches during their spawning migrations despite considerable differences in annual spring flow conditions. Evidence of site-fidelity in migratory paddlefish has occasionally been reported in other populations. In surveys conducted along the Tallapoosa and Cahaba rivers of the Alabama River drainage, none of the recaptured paddlefish were found to move between rivers in subsequent spawning migrations, and some were even recaptured at their original tagging stations (Lein and DeVries 1998). Stancill et al. (2002) also found a high percentage of radio-tagged paddlefish to return to their original capture sites during a multi-year telemetry study conducted in a Missouri River reservoir. Moreover, fish that were tagged in a tributary of the reservoir returned to the tributary even in years where spawning cues were apparently absent.

Although most dramatically demonstrated in salmonids (Dittman and Quinn 1996), the homing tendencies displayed by paddlefish in this study have been similarly documented in other large-river fishes that undergo long-distance spawning migrations. Radio-tagged Gulf sturgeon in coastal drainages of the southeastern United States returned to the same river reaches in subsequent migrations suggestive of a strong home river fidelity (Wooley and Crateau 1985; Heise et al. 2004). Irving and Modde (2000) found radio-tagged migratory Colorado pikeminnow in the upper Colorado River basin to exhibit fidelity to distinct spawning reaches in the Green and Yampa rivers in successive migrations despite sharing the same staging area. Spawning reach fidelity has also been demonstrated for razorback suckers in the Green and Yampa rivers with some migrants bypassing one spawning site to return to a more distant one upriver (Tyus and Karp 1990). Although olfactory recognition has been proposed as a mechanism regulating homing in some of these large-river fishes (Wooley and Crateau 1985; Tyus 1990), it is unknown why some of the fish in our study consistently restricted their migration to specific reaches in the vicinity of the Confluence, while others repeatedly extended their migration to particular areas farther up the YR. If natal homing is operating in paddlefish, unique site-specific cues would have to be imprinted upon at an early life stage because larvae are swept downriver away from incubation areas soon after emergence (Purkett 1961; Russell 1986). Alternatively, individual proclivities to specific reaches may be established through learned behavior in the adult stage, and strengthened by sensory recognition of sites attended to in previous spawning runs (Lucas and Baras 2001). Furthermore, as in the case of the long-distance repeat migrant noted in our study, unique bio-energetic attributes may permit extensive, exploratory migrations in some fish (Secor 1999). Younger mature paddlefish with large quantities of stored fat are typically harvested at higher percentages than older adults with small amounts of fat in the recreational fishery at Intake (D. Scarnecchia, University of Idaho, unpublished). The large amounts of fat observed in these young fish may reflect the availability of surplus energy stores that enable long-distance spawning migrations.

Results from this study indicate that in low or moderate flow years, site-fidelity may be as instrumental as spring discharge in determining reaches frequented by migratory paddlefish. In higher flow years, however, discharge may override site fidelity in dictating locations of spawning fish. If so, this hypothesis would reconcile those studies where paddlefish distribution was associated with spring flows (Purkett 1961; Paukert and Fisher 2001) with those studies in which site fidelity was reported in successive years (Stancill et al. 2002). However, uncertainty remains as to how flow conditions and site-fidelity affect spawning success in this population. For example, because evidence of reproduction in radio-tagged fish was not directly observed, it is unknown whether the seven males that undertook consecutive migrations in 2001 and 2002 spawned in either year. Although annual migrations are not uncommon for male paddlefish (Russell 1986; Lein and DeVries 1998; Stancill et al. 2002), river conditions during the low flow year of 2001 may not have provided the stimuli necessary to induce spawning in these males, most notably in the individual that was contacted at Intake in both years. Long distance migrations and annual spawning may not be compatible reproductive tactics in male paddlefish as has been suggested for male shortnose sturgeon, *Acipenser brevirostrum* (Kieffer and Kynard 1996). In addition, much of the site-fidelity occurred in reaches downriver of YRkm 55. Although substrates considered most suitable for spawning are present along the lower YR, they are more widespread and common above YRkm 55. More information is needed on homing tendencies and potential differential spawning success in paddlefish that migrate to different reaches of the YR to assess the factors that contribute to year-class strength in this population.

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