Spawning Migration of Adult Paddlefish, *Polyodon spathula*, of the Yellowstone-Sakakawea Stock in the Yellowstone and Missouri Rivers, North Dakota and Montana

A Dissertation
Submitted in Partial Fulfillment of the Requirements for the
Degree of Doctor of Philosophy

with a
Major in Fisheries Resources

in the
College of Graduate Studies
University of Idaho

by
Jon Aaron Firehammer
April 2004
Major Professor: Dennis L. Scarnecchia, Ph.D.

AUTHORIZATION TO SUBMIT DISSERTATION

This dissertation of Jon Firehammer, submitted for the degree of Doctor of Philosophy with a major in Fishery Resources and entitled "Spawning migration of adult paddlefish, *Polyodon spathula*, of the Yellowstone-Sakakawea stock in the Yellowstone and Missouri Rivers, North Dakota and Montana", has been reviewed in final form as indicated by the signatures and dates given below. Permission is now granted to submit final copies to the College of Graduate Studies for approval.

Major Professor ______ Date 4-15-04
Dennis Scarnecchia

Committee Members Ernest L Brannon Date 4/15/04
Ernest Brannon

Brian Dennis Date 4/15/04
Brian Dennis

______ Date 4/15/04
Jay O'Laughlin

Eldon H. Franz Date 4/15/04
Eldon Franz

Department Administrator ______ Date 4/21/04
George W. LaBar

Discipline's College Dean ______ Date 4/22/04
Steven B. Daley Laursen

Final approval and acceptance of the College of Graduate Studies

______ Date ______
Katherine G. Aiken

ABSTRACT

Declines in paddlefish populations have been mainly attributed to large river modifications that have created less favorable conditions for reproduction. In order to prevent further alterations to existing reproductive habitat, more information is needed concerning the adaptive strategies used by paddlefish during their spawning migration.

Paddlefish of the Yellowstone-Sakakawea stock (in the unregulated Yellowstone River (YR) and the regulated Missouri River (MR)) were radio-tagged to assess their behavior during migratory and non-migratory periods in 1999-2002. Fish moved extensively both upriver and downriver in association with fluctuating levels of river discharge and suspended sediment during the spring, and were widely distributed along the lower YR in all four years. River selection at the confluence of the MR and YR was also associated with increasing levels of discharge and turbidity. Although fish ascended the YR 82% of the times when moving above the Confluence, fish were occasionally contacted in the MR above the Confluence for short periods of time. The extent of the migration did not advance further up the river system in higher than in lower flow years. Only four of sixty-nine paddlefish were contacted within 15 km of the Intake diversion dam (114 km up the YR) during the study. Movements exhibited by repeat migrants suggested evidence of site fidelity. The observed migratory behaviors may be tactics that have evolved in paddlefish in their unpredictable large-river environments.

A passive egg sampling technique was developed in order to confirm egg incubation sites for paddlefish along the lower YR. In 2001 and 2002, 130 Acipenseriform eggs were collected along the suspected incubation reach; 99% of the identifiable eggs were genetically confirmed as paddlefish. During both years, egg catch-per-unit-effort (CPUE) peaked in mid-June after peak periods of YR discharge. Temperatures were between 15-22°C during periods in which eggs were collected. Eighty-three percent of the eggs were found on collectors retrieved from the channel thalweg. However, mean egg counts were low (< 4 eggs/collector) suggesting either collector inefficiency, the inability to place collectors near concentrations of spawning paddlefish, or the distribution of spawning effort over a large portion of the lower Yellowstone River.

ACKNOWLEDGMENTS

I thank my graduate advisor, Dr. Dennis Scarnecchia, for his guidance throughout the preparation of this dissertation, and Drs. Ernest Brannon, Brian Dennis, Eldon Franz, and Jay O'Laughlin for serving on my graduate committee and for their constructive comments during the review process. I also thank Greg Power and Fred Ryckman for their insight and advice throughout this project. I also extend my appreciation to those who helped collect and analyze data: Shane Shefstad, Brett Bowersox, Sheila Koerner, and Rodney McKinnon for their assistance in the field; Steve Fain and Dyan Straughan at the U.S. Fish and Wildlife Service National Forensics Laboratory in Ashland, Oregon for their technical expertise; and the Nez Perce tribe for providing field materials. I also express my gratitude to Matt Stone, Trey Parker, friends, and especially family members for their encouragement and support in maintaining my equanimity throughout this dissertation. Most importantly, I love my wife Susan for her enduring patience, her calming disposition, and her selfless thoughtfulness that keep me inspired. Funding for this work was provided by the North Dakota Game and Fish Department.

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INTRODUCTION

The North American paddlefish (*Polyodon spathula*) is a large and ancient zooplanktivorous fish that is distributed along the Mississippi River system and selected Gulf slope drainages (Russell 1986). This species, along with the Chinese paddlefish (*Psephurus gladius*) of the Yangtze River drainage, are the only two remnants of an ancient family of fishes, Polyodontidae, whose ancestors first arose around 150 million years ago (Lu 1994). Paddlefish have been present in North America waters for over 60 million years, indicated by the fossil remains of an extinct genus, *Paleopsephurus*, recovered in late Cretaceous Montana deposits (Bemis et al 1997). Paddlefishes, along with sturgeons (Acipenseridae), are the two extant families that comprise Acipenseriformes, an holoarctically distributed relict order of bony fishes that is characterized by a cartilaginous skeleton, heterocercal tail, rostrum, spiral valve intestine, a well-developed spiracle, and a notochord that is retained in adults (Billard and Locointre 2001; see Bemis et al. (1997) for a more thorough discussion of phylogenetic relationships within this order).

Unlike sturgeons, paddlefish are usually regarded as freshwater fishes, although individuals have occasionally been found to move between coastal rivers (Graham 1997). Paddlefish (hereafter, paddlefish refers to *P. spathula* unless otherwise indicated) traditionally occupied slow-moving large river habitats, such as backwaters, oxbow lakes, and braided side-channels, where both juveniles and adults reared throughout most of their lives (Stockard 1907; Alexander 1915; Hoxmeier and DeVries 1997). They have evolved unique characteristics that have allowed them to exploit the zooplankton-rich resources established in these low-velocity off-channel habitats. Unlike other genera within Acipenseriformes, *Polyodon* have long thin gill rakers that accommodate an efficient filter-feeding foraging strategy (Grande and Bemis 1996). Although young-of-the-year paddlefish selectively feed on zooplankton when exogenous feeding commences (Ruelle and Hudson 1977), gill rakers are fully functional by the end of the first summer of growth (Rosen and Hales 1981; Michaletz et al 1982). Paddlefish have also adopted a specialized sensory system to effectively feed in the naturally turbid backwaters of their habitats. An elongated rostrum, which was once believed to be used to dislodge organisms from river bottoms (Alexander 1914), acts as an antennae to locate prey items: the electrosensory ampullae, located along the rostrum, head, and operculum flaps, are able to detect the weak electric fields generated by zooplankton (Wilkens et al 1997).

The life-history characteristics that have evolved within paddlefish also reflect the dynamic nature of their large-river environments. In response to the high degree of variability in reproductive success, growth has been favored over early maturation to provide a long reproductive life-span (Murphy 1968; Schaffer 1974; Roff 1984). Growth rates are rapid during early rearing periods with females generally growing faster than males (Rosen et al. 1982). Males mature at 4-10 years and females mature relatively later at 6-16 years (Jennings and Zigler 2000). The disparity within both sexes reflects the later maturation in northerly than in southerly populations (Carlson and Bonislawsky 1981). The large body size attained through delayed maturation minimizes adult mortality and, in females, accommodates high levels of fecundity both of which contribute to increased reproductive output (Winemiller and Rose 1992). Reported average weights for females range from 13.7 kg in the Alabama River drainage (Lein and Devries 1998) to 25.0 kg in the Yellowstone River, MT (Rehwinkel 1978; Scarnecchia et al. 1996). Much of the weight is due to the large number of eggs produced, as average weight-specific fecundities have been estimated at around 9,500 to 24,000 eggs per kg of body weight (Reed et al. 1992; Lein and DeVries 1998). Iteroparity and longevity in paddlefish also offset the high probability of annual recruitment failure. Although data indicate that mature males of some populations may not undergo spawning migrations in consecutive years, it is suggested that males are capable of spawning annually (Russell 1986). Females, on the other hand, likely spawn every 2-5 years due to the time and energetic investment necessary to develop mature ova between spawns (Russell 1986). Paddlefish are long-lived and it is not uncommon to find fish older than 15 years in many populations (Russell 1986). In some of the more northerly populations, aging studies have found individuals older than 40 years (Scarnecchia et al. 1996).

The spawning migration is another life-history characteristic of paddlefish that enhances reproductive success in variable large-river environments. Seasonal spawning migrations have been considered a behavioral strategy by which adults exploit the temporal periodicity in river conditions that optimizes early-life history survival (Northcote 1978; Welcomme 1979; Leggett 1985; Dodson 1997). Researchers have found paddlefish spawning migrations to coincide with increasing photoperiod, temperature, and discharge during the spring (Purkett 1961; Pasch et al 1980; Berg 1981; Russell 1986; Lein and DeVries 1998; Paukert and Fisher 2001). As in other spring spawners, warming temperatures synchronize emerging larval fish with favorable growing conditions (Jobling 1995). Increasing levels of discharge provide adequate current velocities to ensure the inundation and aeration of clean, well-swept gravel bars over which paddlefish broadcast their adhesive eggs (Purkett 1961; Pasch et al. 1980).

Additionally, sufficient levels of discharge may also aid the downriver transport of larval fish (which hatch in 6 to 12 d; Yeager and Wallace 1982), and maintain the connection between main channel and off-channel habitats that larval fish use as nursery habitats (Russell 1986). High-levels of spring discharge have been shown to be positively associated with year-class strength in various paddlefish populations (Wallus 1986; Hoxmeier and DeVries 1997; Paukert and Fisher 2001).

The spatial heterogeneity in riverine habitats, with often widely separated foraging and spawning habitats, also likely contributes to the behaviors exhibited by migratory paddlefish (Northcote 1984; Rosen et al. 1982; Lucas and Baras 2001). Paddlefish have been found to cover long distances with individuals in some river systems moving over 300 km upriver to reach spawning grounds (Russell 1977). However, finer scales of spatial variability in spawning tactics are generally unknown. Although spawning reaches have been identified in some regulated river systems (Pasch et al. 1980; Wallus 1986; Lein and DeVries 1998), they have yet to be delineated for most paddlefish populations (Jennings and Zigler 2000). It remains unclear whether adults utilize the same restricted spawning sites during subsequent migrations (Stancill et al. 2002), or reproductive effort is widely distributed over larger reaches as has been found in other large-river fishes (Khoroshko 1972; McAda and Kaeding 1991; Modde and Irving 1998; Fox et al. 2000). Much remains to be learned about the adaptive significance of behaviors exhibited by individual paddlefish during their spawning migration.

Currently, paddlefish are found within twenty-two states of the central and southeastern United States. However, their range has been diminished from historic distributions and former peripheral populations have been extirpated in Maryland, New York, North Carolina, and Pennsylvania (Graham 1997). Abundance has also been reduced, even in areas once considered strongholds for paddlefish (Hoxmeier and DeVries 1996). Catch records indicate that the commercial harvest of adults has declined by 60% during the last century, with some individual populations exhibiting a 95% decrease (Gengerke 1986). As of 1994, only six states still allowed commercial fisheries for paddlefish (Graham 1997).

The declines in range and abundance have been mainly attributed to large river modifications for flood control, navigation, and power production (Sparrowe 1986). These alterations have, in many cases, degraded preferred habitat to create conditions less favorable for paddlefish growth and reproduction. Channelization and flow regulation have eliminated many of the productive side channels, oxbow lakes, and backwaters that had served as nurseries and feeding grounds (Russell 1986). River regulation, which alters temperature and flow regimes, has also negatively affected paddlefish reproduction by disrupting the cues used by paddlefish during the spawning migration (Pasch et al. 1980; Unkenholz 1986; Wallus 1986). In addition, impoundments have impeded adult spawning migrations and inundated suitable spawning habitat (Sparrowe 1986).

The decline in paddlefish populations prompted a petition in 1989 to list the species as federally endangered under the Endangered Species Act. However, the species was reclassified in 1992 as of special concern due to the acceptable status of populations in some states and the lack of information on population demographics in many states (Allardyce 1992). As a result, states were encouraged to conduct investigations to assess the status of their paddlefish populations (Runstrom et al. 2001). Eleven states have classified paddlefish as either threatened, endangered, or of special concern, and ten states have adopted stocking programs to supplement poor natural recruitment in existing stocks (Graham 1997).

Paddlefish in Montana and North Dakota are considered a species of special concern. Of considerable interest is the Yellowstone-Sakakawea stock, one of the last naturally-reproducing populations in the United States that sustains an annual harvest. This stock has supported a significant recreational fishery along the Yellowstone and Missouri rivers in eastern Montana and western North Dakota over the past 35 years. The increase in adult recruitment since 1962 was mainly attributed to increased productivity associated with the creation of Lake Sakakawea (a main-stem Missouri River reservoir created by the closure of Garrison Dam in 1953; Scarnecchia et al. 1996). Although year classes likely benefited from the effects of trophic upsurge during the years in which the reservoir was filled, recent information from age structure studies suggests that recruitment in the early 1990's may not be as strong (Scarnecchia et al. 1996). In 1994, state fish and game agencies in North Dakota and Montana developed a cooperative management plan for this stock (Scarnecchia et al. 1995). Due to the lack of information concerning stock-recruitment relationships, plan objectives included increasing the understanding of relationships between paddlefish ecology and year-class strength. Assessing the potential impacts of river system modifications at various life-history stages was emphasized within the stated objectives.

This dissertation addresses questions concerning the relationship between paddlefish behavior during the adult spawning migration and reproductive success. This is not to diminish the importance of other early life-history stages in influencing recruitment dynamics. Annual variability in reservoir levels has been shown to influence age-0 feeding ecology and could affect growth and mortality rates of juvenile paddlefish (Fredericks 1994). Studies have also revealed predation by native and introduced species on age-0 paddlefish which may adversely impact year class strength (Mero et al. 1994; Parken and Scarnecchia 2002). However, information gained from this research would yield insight into habitat requirements for spawning paddlefish, and provide a better understanding of the impacts of river modifications and regulation on adult migratory behavior.

Previous studies have indicated that the majority of adult paddlefish ascend the unregulated Yellowstone River rather than the regulated Missouri River during spring periods of high discharge (Robinson 1966). Although temperature, turbidity, and discharge all play a role within the Yellowstone-Missouri system, the stimuli inducing both the migratory response and the selection of the spawning river are not well understood (Rehwinkel 1978). Also unclear is the influence of the annual flow regime on the strength (i.e. number of paddlefish) and extent of the spawning migration as it relates to reproductive success. There is also a lack of information concerning the reaches used as spawning habitats within the Yellowstone-Missouri river system. Although larval sampling efforts have demonstrated paddlefish reproduction in the lower Yellowstone River (Gardner 1996), egg incubation sites have not been confirmed. It is unknown whether paddlefish repeatedly use spawning sites confined to specific reaches, or if spawning activity is indeterminate with sites widely distributed along the lower Yellowstone River.

Behavioral variability amongst migratory individuals also may exist within the Yellowstone-Sakakawea paddlefish stock. Although the majority of paddlefish are assumed to rear and overwinter in Lake Sakakawea, recaptures of jaw-tagged paddlefish have documented adults in habitats upriver from the reservoir throughout the year (F. Ryckman, North Dakota Game and Fish Department, Williston, North Dakota, pers. comm.). This may indicate the existence of different spawning migration patterns as has been found for populations of sturgeon (Bemis and Kynard 1997). Also, data collected over the past number of years indicates a difference in the age composition between migratory paddlefish harvested at Intake, Montana and in the North Dakota fishery (D. Scarnecchia, University of Idaho, pers. comm.). The factors contributing to this difference and the possible effects it may have on reproductive success and the two fisheries have not been determined.

This dissertation consists of two chapters focusing on different aspects of the Yellowstone-Sakakawea paddlefish spawning migration. The first chapter considers the intra-annual and inter-annual patterns in migratory behavior with respect to variable river conditions along the Yellowstone and Missouri Rivers. The spatial and temporal aspects of paddlefish spawning activity, addressed through the development of an egg sampling technique, is considered in the second chapter.

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CHAPTER 1. Migratory behavior of adult paddlefish in the Yellowstone and Missouri Rivers, North Dakota and Montana

ABSTRACT

Paddlefish, *Polyodon spathula*, of the Yellowstone-Sakakawea stock (in the unregulated Yellowstone River and the regulated Missouri River) were radio-tagged to assess their behavior during migratory and non-migratory periods in 1999-2002. The objectives were to determine how paddlefish responded to temporal and spatial changes in river conditions during the spawning migration, and assess the strength and extent of the migration in relation to the annual flow regime. Paddlefish moved extensively both upriver and downriver in association with fluctuating levels of river discharge and suspended sediment during the spring. This behavior resulted in their widespread distribution along the lower 50 km of the Yellowstone River during late spring of all four years. River selection at the confluence of the Missouri and Yellowstone Rivers was also associated with increasing levels of discharge and turbidity. Paddlefish ascended the unregulated Yellowstone River 82% of the times when moving above the Confluence. Although paddlefish were also occasionally contacted in the Missouri River above the Confluence, most forays into the Missouri were of short duration as fish were contacted less than a week afterward in the Yellowstone River. The magnitude of Yellowstone River discharge during the spring did not correlate with the extent of the upriver migration; the spatial distribution of tagged paddlefish did not advance further up the river system in higher than in lower flow years. Throughout the study period, only four of sixty-nine paddlefish were contacted within 15 km of the Intake diversion dam (114

km up the Yellowstone River); one of the four had been contacted within this reach in 3 different years. Behaviors exhibited by repeat migrants suggested tendencies to migrate specific distances and evidence of site fidelity. The observed seasonal movement patterns may be reproductive tactics that have evolved in paddlefish in their unpredictable large-river environments.

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). 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). However, adults undergo extensive upriver migrations in the spring to access suitable spawning habitats that are often widely separated and distinct from foraging and overwintering habitats (Rosen et al. 1982). In contrast to the low-velocity off-channel non-spawning habitats, spawning reaches are often characterized by fast-flowing reaches with well-swept gravel bars (Purkett 1961; Pasch et at. 1980). Spawning migrations often coincide with a specific combination of environmental stimuli including increasing temperature (Purkett 1961; Russell 1986; Lein and DeVries 1998) and discharge (Pasch et al 1980; Berg 1981; Paukert and Fisher 2001). Because the environmentally-cued spawning migration likely evolved as a behavioral strategy to maximize reproductive success in paddlefish (Leggett 1985; Dodson 1997), it has been considered important for the persistence of self-sustaining populations (Unkenholz 1986).

While paddlefish remain widely distributed within twenty-two states of the central and southeastern United States, peripheral populations have been extirpated and abundance has been reduced in many other stocks (Graham 1997; Jennings and Zigler 2000). The declines in range and abundance have been mainly attributed to large river modifications that have created conditions less favorable for reproduction (Sparrowe 1986; Unkenholz 1986). Impoundments have caused the siltation of and blocked access to spawning habitats, and have altered both river temperatures and the natural hydrograph. Cold, hypolimnetic releases from reservoirs have been implicated in both the delay and inhibition of spawning in adults (Pasch et al. 1980; Wallus 1986), whereas flow manipulations can disrupt spawning cues, dessicate inundated spawning sites, and affect larval survival during downriver transport to nursery habitats (Russell 1986).

Discharge has been considered an important determinant of reproductive success in paddlefish (Wallus 1986; Hesse and Mestl 1993; Hoxmeier and DeVries 1997). However, its influence on migratory behavior remains unclear. The lack of upriver movement observed during low flow years indicates that the magnitude of spring discharge plays a role during the spawning migration (Moen et al. 1992; Paukert and Fisher 2001). Though discharge thresholds have been suggested for various stocks (Russell 1986; Wallus 1986), spawning has been found to occur at river flows lower than that previously reported (Lein and DeVries 1998). The duration of high spring flows has also been suggested as an equally important factor in determining the extent, as well as the success, of the spawning migration (Elser 1977; Purkett 1961).

In order to recover or maintain naturally-reproducing stocks, it is necessary to better understand the influence of discharge and other river conditions on the paddlefish spawning migration and how it contributes to reproductive success. However, studies conducted along regulated rivers may not always reveal the range of migratory behaviors capable of being expressed within a stock. For example, dams tend to concentrate spawning adults in tailwater habitats during the spring (Southall and Hubert 1984; Stancill et al. 2002; Zigler et al. 2004), and hence inhibit the potential dispersive movements of migrants. In addition, the regulation of spring discharge below dams confounds the interpretation of movement observed during the migration. On the other hand, studying the patterns of movement along an unregulated river may provide insight into some of the adaptive behaviors that have evolved in paddlefish to account for the temporal and spatial variability in their large-river reproductive environment.

The Yellowstone-Sakakawea paddlefish stock in eastern Montana and western North Dakota is one of the last naturally-reproducing populations in the United States that sustains an annual harvest. This stock has supported a significant recreational fishery along the Yellowstone and Missouri rivers in eastern Montana over the past 35 years and in western North Dakota for the past 10 years. The success of this stock has been mainly attributed to the productive rearing environment of Lake Sakakawea (a main-stem Missouri River reservoir created by the closure of Garrison Dam) and the access to spawning habitat along the lower Yellowstone River (Scarnecchia et al. 1996). Due to the absence of main-stem dams, the Yellowstone River has retained much of the natural variability in temperature, discharge, and sediment dynamics that have been considered important for successful paddlefish reproduction. In contrast, river dynamics along the stretch of the Missouri River that is accessible to paddlefish have been altered by dam construction. Therefore, a unique research opportunity exists to observe migratory behavior under both relatively natural and regulated river conditions, and gain a better understanding of the effects of river modifications on movement patterns.

Previous studies have indicated that the majority of adult paddlefish ascend the Yellowstone River rather than the Missouri River during the spawning migration, and that fish have been found further upriver during high flow than during low flow years (Robinson 1966; Rehwinkel 1978). Although temperature, turbidity, and discharge all play a role within the Yellowstone-Missouri system, their influence on both the migratory response and the selection of the spawning river are not well understood. Also unclear is the influence of annual river conditions on the strength of the migration (i.e. the number of paddlefish cued to migrate) and the spatial distribution of migrants along the lower Yellowstone River and its relation to reproductive success.

A radio telemetry study was conducted during 1999-2002 to examine the migratory behavior of Yellowstone-Sakakawea adult paddlefish. The objective of the study was to determine how annual river conditions influence the temporal and spatial distribution of spawning paddlefish along the Yellowstone and Missouri Rivers. This objective included assessing the direction and rates of movement in relation to changing river conditions during the spawning migration, comparing the number of fish ascending either the Yellowstone or Missouri Rivers with the difference in the thermal and flow regime between the two rivers, and assessing the strength and extent of the migration in relation to the annual flow regime. Results were to be interpreted for their implications for annual reproductive success.

STUDY AREA

Paddlefish from the Yellowstone-Sakakawea stock typically rear in Lake Sakakawea, a 156,000 ha Missouri River impoundment in western North Dakota created by the closure of Garrison Dam in 1953. Adults ascend to the headwaters of the reservoir and migrate upriver during the spring in preparation for spawning. Paddlefish have access to 350 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 110 rkm of the Yellowstone River from its confluence with the Missouri River (hereinafter referred to as the Confluence) upriver to the Intake Diversion Dam near Glendive, Montana (Figure 1). The study area consisted of three reaches: the Yellowstone River (YR), the Missouri River above the Confluence (MRAC), and 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 the number of river kilometers above and below the Confluence along the Missouri River, respectively.

The YR has remained mostly unregulated, though two low-head irrigation diversion dams exist at Intake (YRkm 114) and Cartersville (YRkm 382). The river has thus retained a quasi-natural hydrograph with elevated levels of discharge and sediment load during the spring. Average discharge during June at Sidney, Montana (YRkm 47) over the period 1910-2002 has been 1100 m^3/s (USGS 2003). River reaches below the Intake diversion dam contain multiple islands and alluvial channel bars with swift current and substrate consisting primarily of cobble and gravel. Although in-channel features remain common along the lowermost 40 km of the river, sand replaces gravel as the predominant substrate (Bramblett 1996).

The MRAC extends 300 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 the completion of the dam, average discharge during June at Culbertson, Montana (MRkm 63) over the periods 1941-51 and 1958-2002 has been 275 m^3/s (USGS 2003). Although gravel and cobble are prevalent in the upper reaches due to downcutting, the lower 250 km are characterized by sediment deposition with numerous shifting sand bars (Gardner and Stewart 1987). Channel gradient along the MRAC is generally lower than that along the YR (Tews 1994).

The MRBC section runs freely for approximately 25 to 80 rkm, depending on reservoir pool elevation, until it reaches the headwaters of Lake Sakakawea (Scarnecchia et al. 1996). Compared to the MRAC, discharge and sediment levels along the MRBC are typically higher during the spring due to the influence of the YR. Sand bars are common along this reach with channel depths typically greater than those along the YR and MRAC reaches.

METHODS

Field procedures

Radio transmitters were surgically implanted into adult paddlefish during the spring and fall of 1999 and the fall of 2000 (hereinafter these groups of tagged fish will be referred to as S99, F99, and F00 fish, respectively). Fish 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. It was assumed that paddlefish captured in this river reach would participate in the spring migration. In addition, fish captured below the Confluence, rather than above, prevented the selection of adults that had already migrated into one river over the other. Upon contact with the 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.

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 d (hereinafter fish will be identified by their abbreviated frequency; e.g., 49.011 as 011). All transmitters, running on a pre-programmed 12 h on/off cycle to conserve battery life, were activated to transmit between 0700 and 1900 h. Transmitters of three different dimensions were implanted during the study. Sex-specific large-diameter transmitters were used for S99 fish: 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 F99 and F00 fish were lighter (100 g), longer (17.0 cm), and of smaller diameter (2.0 cm) than those implanted into S99 fish to accommodate a smaller incision and fewer sutures during implantation. Radio transmitters weighed less than 2% of the body weight for all tagged fish (Winter 1996).

Surgical procedures were slightly different between spring and fall tagging. Throughout the procedure, river water was pumped across the gills to maintain a constant supply of oxygen. An initial incision was made about midway between the insertion of the pectoral and pelvic fins off the ventral midline of the fish. A smaller incision was made for F99 and F00 fish (3-4 cm) than for S99 fish (6-7 cm) because of the smaller diameter of the transmitters used for fall-tagged fish. A modification of the shielded-needle technique was then used to create an exit site, about 5.0 cm posterior to the initial incision, to guide the transmitter antenna through the body wall (Ross and Kleiner 1982). After insertion of the transmitter into the body cavity, the incision was closed with non-absorbable sutures. Whereas 5-8 sutures were required to close the incision for S99 fish, only 3-5 sutures were required for F99 and F00 fish. In addition, mattress sutures were used for fall-tagged fish. With this method, each suture ran through the body walls twice to hold the walls together at two points and to relieve tension on the suture. After closure, antibacterial ointment was administered along the incision and the exit site to prevent infection. Fish were then held in the river and released after active movement suggested recovery.

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 occasionally conducted, particularly along the MRAC due to its inaccessibility by boat, to determine the general distribution of tagged fish along the river system. 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 system (indicating movement back into the reservoir) because the radio transmitters were not easily detected at reservoir depths. During the fall and winter, unit 3 was tracked to identify overwintering areas below the Confluence. Searches were conducted only 1-3 times per month because of the general lack of movement during this time. Geographical coordinates were recorded for all contacted fish using a global positioning system receiver.

River conditions were assessed by using information obtained from gauging stations, or from data collected during weekly searches. Daily YR discharge (m^3/s) and suspended sediment (mg/L) data were obtained from the United States Geological Survey (USGS) gauging station near Sidney, Montana (YRkm 47), and daily temperatures were obtained from a data logger positioned at YRkm 13.5. Daily MRAC discharge (m^3/s) and temperature were obtained from the USGS gauging station near Culbertson, Montana (MRkm 63) and a data logger positioned at MRkm 6, respectively. Because daily suspended sediment data was not available for the MRAC, turbidity was measured along both rivers above the Confluence during weekly searches in order to draw comparisons between the two rivers. Daily MRBC discharge was estimated as the combined discharge from the YR and MRAC. In order 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.

Data Analyses

Field coordinates were overlaid onto a digitized map of the river system using geographic information systems software (ARC/INFO, Environmental Systems Research Institute, Inc., Redlands, California), and paddlefish contacts were each assigned a river kilometer. Positive and negative values indicated the number of river kilometers above and below the Confluence, respectively. The distance moved by a fish was estimated as the number of river kilometers between contacts; positive and negative distances represented upriver and downriver movements, respectively. Movement rate (km/d) was calculated by dividing the movement distance by the number of elapsed days between consecutive contacts. In order to minimize the underestimation of movement rates, only those movements in which elapsed periods between contacts were less than or equal to 7 d were used in analyses.

Paddlefish movement was initially characterized by describing general changes in the distribution of contacts during the spring. For all four years, the YR flow regime was separated into two distinct periods: an initial period of fluctuating, slowly increasing discharge, and a latter period of rapidly increasing discharge (Table 1). Peak discharge and levels of suspended sediment were typically higher in the latter than the former period for all four years. The distribution of contacts along the river system was compared between flow periods for all four spring migrations.

Paddlefish movements were then analyzed in relation to temporal changes in river conditions. As has been expressed by others, migratory fish may be more responsive to the relative change than to absolute levels of river variables (Harden-Jones 1968; Trepanier et al. 1996). Furthermore, it was hypothesized that paddlefish exhibited reactive responses throughout their spawning migration rather than goal-oriented behavior. Reactive responses were assumed to involve changes in direction or movement rate with respect to changes in river conditions. In contrast, goal-oriented behavior was assumed to involve directed movements toward spatially-explicit spawning grounds once the migration was initiated regardless of ensuing changes in river conditions. In testing this hypothesis, only data from the spawning migrations of 2000 and 2001 were used because of the lack of short-term movement data for 1999 and 2002.

In order to test for an association between directional movement and changes in discharge, suspended sediment, or river temperature, only those movements during periods of monotonically increasing or decreasing river conditions were included. Under this restriction, a movement was included in the analysis as long as each river variable was either stable, increasing, or decreasing during the period in which a fish was contacted on consecutive occasions. The change in river conditions for each movement distance was calculated using the following equation:

$$X_{\Delta} = \mathrm{Log}(X_{(t)} / X_{(t-d)}); \qquad (1)$$

where,

$X_{(t)}$ = river variable value on day t (latter day of contact); and

$X_{(t-d)}$ = river variable value on day t-d (former day of contact).

The quotient, rather than the difference, was used in order to distinguish between similar increments or decrements in river variables. For example, paddlefish may respond differently to an increase in discharge from 300 to 600 m^3/s than to an increase in discharge from 1200 to 1500 m^3/s. Although both represent an increase of 300 m^3/s, the first is doubled while the second is increased only by a factor of 1.25. Log transformations were used in order to normalize the distribution of the quotients. Because fish were contacted infrequently along the MRAC, only those movements along the MRBC and YR were included in the analysis. In addition, YR variables were used in calculations for those fish that moved between the MRBC and YR during consecutive contacts.

Regression models were constructed to determine the relative importance of discharge, suspended sediment, and river temperature in describing directional movement. Because the explanatory variables were likely to be correlated, the variance inflation factor (VIF) was used to detect for multicollinearity. If multicollinearity was detected ($VIF \geq 2$; Graham 2003), a principal components analysis (PCA) was conducted to identify orthogonal principal components that described the variability in the original explanatory variables. Scores of the principal components were then used as new explanatory variables in the regression models (Johnson 1998). All of the principal components were used (not just those components with high eigenvalues) so that explanatory power was not lost during analysis (Graham 2003). In order to prevent bias toward fish that were frequently contacted, each movement was inversely weighted by the total number of movements by that fish included in the analysis. Response variables were log transformed if model residuals indicated non-normality.

Model selection analysis using the information-theoretic approach was used to evaluate the relative plausibility of candidate regression models (Burnham and Anderson 1998). Candidate models included the reduced model with no explanatory variables and those models with different subsets of the newly created principal component scores. Akaike's Information Criteria, adjusted for small sample size (AIC_c), was used to determine the best approximating model, or the model with the lowest AIC_c. AIC_c differences between the best model and other candidate models (ΔAIC_i) were calculated and used to judge the relative likelihood of each model as being the best: a $\Delta AIC_i \leq 2$ indicated that the model had substantial support as the best model, whereas a $\Delta AIC_i > 10$ indicated that the model had essentially no support (Burnham and Anderson 1998). The ΔAIC_i was also used to calculate the Akaike weight (w_i) for each model according to the following equation:

$$w_i = \exp(-0.5*\Delta AIC_i)/\sum (\exp(-0.5*\Delta AIC_i)) \qquad (2)$$

Only those models with a ΔAIC_i less than 10 were included in the summation term in the equation. Akaike weights were used to judge the relative importance of each explanatory variable in describing paddlefish movement distance by summing up the w_i's for each of the models that contained the respective explanatory variable.

In order to test for an association between upriver movement rate and the rate of increasing river discharge, movement rates were compared between different periods of increasing discharge within a sample year. Only those fish that were contacted during both periods of increasing discharge within a year were used in the analysis to account for potential individual differences in movement patterns. If more than one movement rate was estimated for a fish during a discharge period, the average of the movement rates was used. For the 2000 migration, comparisons were drawn between the gradual rise in discharge (187-365 m^3/s) that occurred over a 13 d period from April 26 to May 9 and the rapid rise in discharge (163-997 m^3/s) that occurred over a 13 d period from May 20 to June 2. For the 2001 migration, comparisons were drawn between the gradual rise in discharge (150-240 m^3/s) that occurred over a 5 d period from May 1 to May 6 and the rapid rise in discharge (200-570 m^3/s) that occurred over a 5 d period from May 14 to May 19. Differences in movement rates 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 total number of rkm traversed by male and female paddlefish during the spring spawning migration. This analysis was only conducted for those fish that were still contacted in the river system during June to eliminate the variability associated with those fish that were not found throughout the latter part of the migration. A two-factor ANOVA with year and sex as effects was used to test for differences in the distributions of the cumulative rkm data.

Logistic regression was used to test the hypothesis that river selection by paddlefish was related to differences in river conditions between the YR and MRAC at the time fish moved upriver of the Confluence. 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. In addition, only data from the last three migrations were used because of the lengthy elapsed periods between contacts for fish during 1999. The difference in the rate of change in discharge and the differences in the magnitude of discharge, turbidity, and temperature between the two rivers were chosen as the four predictor variables to be included in the models. Turbidity was used rather than suspended sediment because sediment data was not available for the MRAC. The following equation was used to calculated the difference in the rate of change in discharge between the two rivers:

$$Q_{(Y\text{-}M)} = (X_{\Delta\,(Y)} - X_{\Delta\,(M)}) / d; \qquad (3)$$

where,

$Q_{(Y\text{-}M)}$ = difference in the change in discharge between rivers;

$X_{\Delta\,(Y)}$ = change in discharge for the YR (calculated from equation (1));

$X_{\Delta\,(M)}$ = change in discharge for the MRAC (calculated from equation (1)); and

d = number of elapsed days between consecutive contacts.

A positive $Q_{(Y\text{-}M)}$ indicated that discharge along the Yellowstone River was increasing at a greater rate or decreasing at a lesser rate than along the Missouri River. Likewise, a negative $Q_{(Y\text{-}M)}$ indicated that discharge along the Missouri River was increasing at a greater rate or decreasing at a lesser rate than along the Yellowstone River. The following equation was used to calculate the difference in the magnitude of discharge, turbidity, and temperature between the two rivers:

$$X_{i,(Y\text{-}M)} = \text{Log}\,(X_{i,(Y)} / X_{i,(M)}); \quad (4)$$

where,

$X_{i,(Y\text{-}M)}$ = difference in the magnitude of variable *i* between rivers;

$X_{i,(Y)}$ = variable *i* measured above the Confluence on the Yellowstone River; and

$X_{i,(M)}$ = variable *i* measured above the Confluence on the Missouri River.

Because the exact date a fish moved above the Confluence could not be determined, an average value for $X_{i,(Y-M)}$ was calculated using the inclusive dates of the elapsed time period between contacts.

Similar to the movement distance analysis, principal component scores, created to correct for multicollinearity amongst the original predictor variables, were used in regression analyses. Candidate logistic regression models used the selection of either the YR or the MRAC as the response variable and different subsets of the principal component scores as the predictor variables. In addition, a model with no predictor variables was included to determine if river selection was unrelated to differences in river conditions. Similar to the model selection analysis conducted for movement distance, ΔAIC_i values and w_i's were used to evaluate the relative likelihood of each model as the best approximating model and the relative importance of the predictor variables in determining river selection. The best model was then used to predict the probability that tagged fish would select either the YR or MRAC, and comparisons were drawn to the observed data.

It was also hypothesized that inter-annual differences in the Yellowstone River flow regime would influence temporal and spatial patterns of behavior in migratory paddlefish. The three indices chosen to represent spatio-temporal behavior were last contact date, last contact YRkm, and furthest upriver YRkm. Because paddlefish have been found to move back downriver after spawning (Russell 1986), the last contact date was chosen to represent both the potential date of spawning and the termination of the spawning migration. Similarly, the last contact YRkm was used to indicate the river location where fish may have spawned before exiting the river system. This index was only used as an approximation because fish could have spawned in reaches either upriver or downriver from the last contact position. The furthest contact YRkm was used to assess the influence of the flow regime on the distance paddlefish moved up the Yellowstone River during the spring migration. A two-factor MANOVA was used to determine if either sex or year influenced the spatio-temporal distribution of the three response indices. At first, only those fish that were identified as either male or female were included in the analysis. If sex was determined to be an insignificant factor, all actively migrating fish (including those of unknown sex) were used in the analysis for determining a year effect. The data were first checked to determine if they were distributed according to a multivariate normal distribution and log-transformations were used to correct for problems with non-normality.

RESULTS

Sixty-nine paddlefish were tagged with radio-transmitters during the study period: 25 during the spring of 1999, 22 during the fall of 1999, and 22 during the fall of 2000 (Table 2). Females were typically longer and heavier than males (Table 3). Thirty-one of the 69 fish were females with lengths that ranged from 102 to 127 cm (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 (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 (mean, 103 cm) and 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 (ANOVA; $p>0.1$). Although maturation stage was not determined for the 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-tagged fish were contacted 1397 times during the study period (Table 2). However, 122 of the contacts were from 11 of the 69 tagged fish (16%) that presumably either expelled their transmitters or died. Seven of these eleven fish had been fitted with the large radio-tags during the spring of 1999. Although three of the eleven fish were never found to move upriver during telemetry searches, seven of the eleven fish had moved upriver during the spring following implantation before tag contact indicated probable expulsion. One of the sixty-nine fish was never contacted after it was tagged in the fall of 2000. The other 57 tagged fish remained at large in the river system for periods of 7-1245 d. Variability in tagging dates and the number of years in which tagged fish were contacted in the river system resulted in 2-59 contacts per fish. Six fish were harvested throughout the study period after remaining at large from one week to two years. Two of the tags recovered from harvested fish and one tag recovered in the headwaters of the reservoir were re-implanted into other fish.

Annual flow and thermal regimes

The spring flow regime along the YR exhibited interannual differences in both peak discharge and in the duration of increasing discharge (Figure 2). Peak discharge was highest for 1999 (1509 m^3/s) and lowest for 2001 (680 m^3/s) with intermediate levels of peak discharge in 2000 (997 m^3/s) and 2002 (1093 m^3/s). In addition, fluctuations in YR discharge were less prevalent during 1999 and 2000 than during 2001.

During 1999 and 2000, discharge increased for periods of at least 10 d, whereas periods of continuously rising discharge lasted no longer than 6 days during 2001. MRAC discharge was relatively stable during the spring of all four study years (Figure 2). Peak discharges for the time period April 20- July 15 were 413, 382, 282, and 311 m^3/s for the four consecutive spring/summer seasons.

Although river temperatures generally increased throughout the spring and early summer during all four years, there were inter-annual differences amongst the spring thermal regimes (Figure 2). Whereas YR temperatures typically exceeded 15°C during May of 2000 and 2001, May YR temperatures in 1999 and 2002 fell below 15°C for periods of 14 d. These differences were reflected in the lower number of May degree days calculated for 1999 (446) and 2002 (408) than for 2000 (501) and 2001 (517) (Table 1). Although MRAC temperatures reflected the patterns observed along the YR during all four spring seasons, temperatures were consistently lower along the MRAC than the YR by 0.1-3.6 °C.

Spring contact distribution

The distribution of radio-tagged paddlefish generally moved upriver as spring advanced in all four study years. During early spring periods before the first pulse in YR discharge, fish were typically contacted in reaches below the Confluence (Figures 4, 5). River temperatures were increasing during this time and in excess of 14°C by the end of April. Movement above the Confluence was first detected in all four years during initial periods of rising discharge (Table 1; Figures 3-6). Of those fish that were actively migrating during the four consecutive spring seasons, thirteen (59%), seven (37%), sixteen (67%), and twelve (55%) were contacted above the Confluence at this time (Tables 4-7). During the first three years, contacts were typically distributed within a 75 km reach that extended from MRkm –35 to YRkm 40 (Figures 3-5). In 2002, fish that ascended the YR were only distributed along the lowermost 14 rkm whereas fish that ascended the MRAC were contacted up to MRkm 100 (Figure 6).

During all four springs, a higher percentage of the actively migrating fish were contacted above the Confluence during the latter periods of rising discharge than during the initial periods of rising discharge. Sixteen (76%), eleven (61%), fifteen (68%), and seventeen (77%) fish from the four consecutive spring seasons were contacted above the Confluence during these latter periods. Although 89% of the contacts were distributed along the lowermost 50 rkm of the YR, five, one, three, and three fish were contacted above YRkm 50 during the four consecutive spring migrations (Figures 3-6). Fish were typically not contacted below the Confluence during these latter periods of increasing discharge. Few fish were contacted in the river system by late June and early July during all four years; river temperatures typically exceeded 20°C at this time.

Relationships between movements and river conditions

Paddlefish directional movements were related to the change in discharge and suspended sediment along the river system during 2000 and 2001. During 2000, 20 of the 21 (95%) upriver movements greater than 10 km occurred during periods of increasing discharge and suspended sediment. Of the upriver movements greater than 20 km, 10 of the 16 (63%) occurred during the rapid increase in both river variables from May 20 to June 2, whereas only 3 of the 16 (19%) occurred during the earlier, more gradual increase in both variables from April 26 to May 9. During 2001, 26 of the 28 (93%) upriver movements greater than 20 km occurred during periods of increasing discharge and suspended sediment. Only 4 of the 26 (15%) movements occurred during the earlier, brief rise in both variables from May 1 to May 5, whereas the remaining 22 (85%) movements occurred during the more rapid or more prolonged increases in both variables from May 14 to May 19 and from May 27 to June 6. Similarly, 14 of the 17 (82%) downriver movements greater than 10 km occurred during periods of decreasing discharge and suspended sediment from May 9 to May 20 and from June 2 to June 6, 2000. During 2001, 14 of the 19 (74%) downriver movements greater than 20 km also occurred during periods of declining discharge and suspended sediment; seven of the eight (88%) greatest downriver movements occurred during rapid declines in both river variables from May 19 to May 27.

Model selection analysis supported the importance of discharge and suspended sediment as river variables explaining paddlefish movements. All of the models considered to have substantial support as the best approximating model (i.e. $\Delta AIC_i \leq 2$) included the first principal component as a regressor variable, and, as a result, the first principal component was considered the most important variable in explaining movement during 2000 and 2001 (Table 8). Because both the change in discharge and suspended sediment were strongly correlated with the first principal component (Table 9), this component described periods when both variables were either increasing or decreasing in concert. The second principal component, which was strongly correlated with the change in temperature, was not as important as the first in describing movement.

During 2001, the third principal component was just as important as the first component in explaining movement (Table 8). Because the change in discharge and suspended sediment were weakly but inversely correlated with the third principal component (Table 9), this component described periods when discharge and suspended sediment were not changing in concert. As an example of the variability described by the third component, discharge increased whereas suspended sediment remained relatively stable from May 27 to June 1, 2001. During this time, all of the contacted fish were found to move at least 15 km upriver. However, the interactive effect of discharge and suspended sediment on movement was difficult to interpret when the two variables were inversely changing. For example, discharge increased as suspended sediment decreased from May 25 to May 31, 2000. Only 2 of 11 fish were found to move more than 10 km upriver, whereas the other nine fish had either moved several km upriver or moved downriver.

The association between directional movement and the change in discharge and suspended sediment resulted in repeated directional changes by individual fish during the spring migration. Seven of the 12 (58%) and 14 of the 23 (61%) fish that had moved above the Confluence had been found to ascend the Confluence more than once during 2000 and 2001, respectively (Tables 5 and 6). 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 occasions were two fish contacted within the same rkm on the same date after a previous contact together within an upriver or downriver rkm.

The rate of upriver movement by paddlefish was positively associated with the rate of increase in discharge and suspended sediment during the spring migration of 2001 (Figure 7). Individual-specific movement rates were significantly greater during the rapid increase in discharge and suspended sediment from May 14 to May 19 than during the gradual increase in both variables from May 1 to May 6 (median difference, 9.7 rkm/d; p=0.01). However, individual-specific differences in movement rates were not significant for the 2000 data (median difference, 0.2 rkm/d; p=0.16). Although movement rates of four of the nine fish were twice as great 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, movement rates for the other five fish were either similar during both periods or greater during the earlier than the latter period. The observed differences in movement rate between discharge periods may have been biased by the number of elapsed days used in their estimation. As the number of elapsed days between contacts increased, both the mean level and the variability of the estimated movement rates decreased (Figure 8).

The cumulative number of rkm traversed by paddlefish did not differ between sexes (p=0.62) or years (p=0.63) for the 2000 and 2001 spring migrations (Figure 9). When combining both years of data, the average cumulative rkm for females and males were 162 and 179, respectively. The two greatest cumulative movements were from female fish in the 2000 (310 rkm) and 2001 (292 rkm) migrations. Cumulative movements were not significantly related to either the size of the fish for either sex, or the number of days at large during the spring migration (p>0.1).

River selection

Radio-tagged paddlefish were found to ascend the YR 105 of the 128 times (82%) when consecutive contacts indicated upriver movement from below the Confluence. However, two, four, six, and ten fish were contacted along the MRAC during the four consecutive spring migrations (Tables 4-7). Although fish were typically contacted within the lowermost 5 rkm of the MRAC, one fish was contacted at MRkm 198 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 four years. For 14 of the 17 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 3 fish which had been contacted at least 60 rkm up the MRAC in 2002 were later contacted up the YR 12-18 d afterward.

Paddlefish typically selected the river that was both increasing at a greater rate and had higher average discharge and turbidity than the other river. For example, of those fish that were contacted along the MRAC, contacts often occurred during brief periods of increasing MRAC discharge and decreasing YR discharge (Figures 10-13). Average turbidity and discharge were also typically higher along the MRAC than the YR during these periods. These observations were consistent with model selection results that indicated river selection was best predicted by the model with the first principal component as the regressor variable ($\Delta AIC_i \leq 2$; Table 10). The first principal component accounted for 74% of the variation in the original variables and was strongly correlated with the difference in the rate of change in discharge (0.77) and the differences in the magnitude of discharge (0.88) and turbidity (0.91) (Table 11). On the other hand, the second and third principal components were not considered as important as the first component in predicting river selection (Table 10). The difference in temperature between the two rivers was not considered in the analysis because measured temperatures along the MRAC were never higher than those along the YR during periods when fish ascended past the Confluence.

When using the best approximating model to predict river selection, fish that ascended the YR and MRAC were correctly classified 11 of 15 (73%) and 9 of 11 (82%) times, respectively (Figure 13). Incorrect classifications occurred when flow regimes between the two rivers were relatively similar (i.e. principal component scores between –1.0 and 1.0). For example, three incorrectly classified fish that 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 12). In addition, two other fish had ascended the MRAC during the same two-day period.

Inter-annual migratory behavior

A significant difference in the spatio-temporal distribution of tagged paddlefish was not detected among the four spring migrations (MANOVA, p=0.11; combined data were used since sex was found to be an insignificant factor). Furthest upriver YR contacts were distributed similarly for all four spring migrations; most fish were contacted below YRkm 55 (Figure 15). Although four fish were contacted further than YRkm 55 during the high flow year of 1999, two fish were contacted along this reach during the low flow year of 2001. On only six occasions (3 belonging to one fish) were fish contacted within 15 rkm of Intake (YRkm 114) during the study.

River kilometers where fish were last contacted, as evidence of potential spawning reaches, were also distributed similarly among all four spring migrations (Figure 16). Most of the contacts were widely scattered along reaches downriver of YRkm 55. On various occasions when individual fish were last contacted, other tagged fish were also contacted within the same one km reach. These aggregations, which suggested probable spawning groups, were also widely distributed along the lowermost 50 rkm of the YR and along reaches below the Confluence (Table 12). Of those fish that were last contacted below the Confluence, many were males that had seemingly exited the river early as they were not contacted after the first week in May (Figure 16).

Dates when fish were last contacted, as potential evidence of spawning times, varied throughout our study. Fish were last contacted from April to July; elapsed time periods between last contact dates for the first and last fish were 54, 77, 47, and 61 d for the four consecutive springs (Figure 17). Although surveys in which fish were not contacted were conducted throughout July of 1999 and 2000, surveys were last conducted on June 21, 2001 and July 1, 2002 due to logistical constraints. Therefore, it was difficult to determine when tagged fish still present in the river system during the final survey dates in 2001 and 2002 moved out of the river system.

Although the distributions of last contact dates were not found to be statistically different, there was inter-annual variability in the temporal behavior of tagged fish. Whereas 88% of the fish were still present in the river by June of 1999, only 65, 68, and 74% remained in the river by June of 2000, 2001, and 2002, respectively (Figure 17). In addition, many fish were last contacted during the first two weeks in June of each year after peak periods of YR discharge. However, in association with the coldest May temperatures of all four years, only 31% of the fish from the 2002 migration presumably exited during this brief time period, as compared to 53, 41, and 45 % of the fish from the first three migrations, respectively (Figure17). Moreover, fish were contacted for an extended period of time in 2002 as six fish (32%) were still present in the river system by June 24 (Figure 17).

Twenty-five fish were contacted during at least two of the four spring migrations (Table 13). Of the 25 contacted fish, nine (8 males and 1 female) had been tagged in S99, twelve (5 males, 6 females, and 1 unknown) had been tagged in F99, and four (all males) had been tagged in F00. Females were contacted every two or three years; no females were contacted in consecutive spring migrations. On the other hand, males were typically contacted every other year or in successive years; three males were contacted in three of the four migrations. In addition, some fish exhibited similar behavior during each of the migrations in which they were contacted. Four males (251, 311, 801, and 900) and one female (691) were never contacted further than YRkm 13.5 (Table 13). Furthermore, two of these four males seemingly exited early each year as they were consistently last contacted during the first week in May. On the other hand, one male (571) was contacted within 15 rkm of Intake (YRkm 114) in each of the three years in which it had migrated (Table 13). Six other fish (492, 591, 741, 821, 841, and 910) also displayed some sort of site fidelity, as furthest upriver contacts in repeat migrations were within 10 rkm of each other for each fish (Table 13). This fidelity occurred along a reach from YRkm 28 to YRkm 53.

Fall/winter contact distribution

Twenty, twenty-eight, eighteen, and eleven radio-tagged fish were contacted during the fall/winter periods of 1999, 2000, 2001, and 2002, respectively. All but five of these fish were contacted during the following spring migration indicating the use of the MRBC as staging habitat for migratory paddlefish. Most of the fall/winter contacts were concentrated within specific reaches below the Confluence (Figure 18). Eighty-nine, sixty-nine, and eighty percent of the contacts were distributed within a reach 12-15 km below the Confluence for fall tracking periods of 1999, 2000, and 2001, respectively. Another reach 33-36 km below the Confluence had accounted for 11 and 12% of the contacts during the falls of 2000 and 2001, respectively. Fish did not move much during the fall; 80, 71, and 86% of the movements were less than 1.5 rkm during 1999, 2000, and 2001, respectively (Figure 19). Most of the movements greater than 1.5 km upriver of downriver were due to fish moving between the two staging reaches below the Confluence. Because other reaches of the study area, including the reservoir, were not surveyed during the fall/winter period, other staging sites likely existed. Although not contacted during fall or winter, one, two, and five fish were contacted during the following spring migrations of 2000, 2001, and 2002, respectively.

DISCUSSION

Radio-tagged adult paddlefish of the Yellowstone-Sakakawea stock moved extensively both upriver and downriver during the spring migration coincident with periods of increasing and decreasing discharge and suspended sediment, respectively. 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). None of these studies mentioned the incidence of temporary downriver movements corresponding to intermittent periods of declining discharge during the spawning migration. Zigler et al. (2003), however, found paddlefish along the Wisconsin River to synchronously move downriver out of staging habitats as spring discharge increased. In contrast, several studies conducted along navigation pools of the upper Mississippi River did not detect a relationship between change in discharge and coordinated directional movement (Southall 1982; Moen et al. 1992; Zigler et al. 2003).

The difference between the coordinated directional movement noted in this study and the lack of synchronized movements noted in other studies may have been due to differences in the maturation status of tagged paddlefish. 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. On the other hand, 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 not respond to cues such as increasing discharge.

The modifications along regulated river systems may have also contributed to the differences in movement patterns observed between this and other studies. In other studies, paddlefish were often concentrated below dams during the spring and were prevented from moving upriver during periods of increasing discharge (Southall 1982; Moen 1989). Zigler et al. (2003) also suggested that Prairie du Sac Dam, which prevented the upriver movement of fish staging in its tailwaters, may have been a factor in the unusual synchronized downriver movement noted during the spring. Modified flow regimes that suppress migratory cues may have also affected paddlefish behavior in these studies. Moen et al. (1992) suggested that the modest levels of regulated discharge in their study may have not been sufficient to stimulate coordinated upriver movements by tagged fish.

The directional changes associated with changing levels of discharge demonstrated by paddlefish in this study also does not seem to be a common pattern of behavior found in the phylogenetically-related sturgeons, 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 pre-spawning migration.

The choice of river that paddlefish ascended was also related to differences in the flow regimes between the two rivers. The tendency for fish to ascend the YR rather than the MRAC was associated with higher levels of turbidity and discharge along the unregulated YR. Robinson (1966) and Rehwinkel (1978) reported similar findings for this stock. Paddlefish in this study also ascended the MRAC during brief periods when turbidity and discharge were higher there than in the YR. Similarly, Paukert and Fisher

(2001) found differing spring flow regimes to influence river selection by migratory paddlefish. They suggested that the earlier peak in discharge along the Salt Fork River contributed to fish ascending the Salt Fork 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 telemetered 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 higher levels of discharge along the river that was ascended.

The observed patterns of river selection may have consequences for proposed releases of water from Fort Peck Reservoir that increase Missouri River discharge during the spring. Paddlefish that ascended the MRAC during brief periods of increasing discharge 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.

Results from this study indicate that discharge and suspended sediment appear to be important stimuli for pre-spawning movements of paddlefish. However, it is unclear how these two variables interact to stimulate that behavior. Fish moved upriver as discharge increased amid stable concentrations of suspended sediment; they also moved downriver as discharge increased amid decreasing concentrations of suspended sediment. Because these two river variables are often highly correlated during the spring, changing concentrations of suspended sediment may be used as a migratory cue to indicate levels of discharge that facilitate access to upriver spawning grounds and promote reproductive success. Alternatively, paddlefish may be cueing on a river variable correlated with both discharge and suspended sediment but not addressed in this study.

In contrast, results from this study indicated that river temperature was not influential in determining directional movement of pre-spawning 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 were typically over 14°C and rising. Paukert and Fisher (2001) also found 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). However, as has been suggested for other migratory fishes, temperature and photoperiod are more likely to be instrumental in timing the general migratory response to other stimuli (e.g. Northcote 1984; Leggett 1985; Smith 1985; Whalen et al. 1999), rather than influencing immediate directional movements.

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 (such as piloting and compass orientation) that bias their movement toward the appropriate heading (McKeown 1984; Neill 1984). However, spawning habitat in dynamic large-river environments may be relatively widespread but unpredictable from year to year, and thus specialized behavior that guide 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 directional changes observed during this study.

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. Scarnecchia, University of Idaho, pers. comm.), 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 (D. Scarnecchia, University of Idaho, pers. comm.).

The distribution of last contact river positions also suggests that spawning activity was not concentrated in specific sites but widely distributed over the lower YR. Although no direct evidence that tagged fish spawned was found, 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 spread out 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 distribution of last contact dates from late April to early July also implied an extended period of spawning activity for paddlefish in this study. This variability in inferred spawning times may have been due to reproductively ready fish at various stages of gametic development in early spring. It would not be that unusual for individuals to be somewhat out of phase with each other due to the relatively long period of time for gonadal recrudescence in paddlefish (i.e.1-2 years for males and 2-5 years for females (Russell 1986)). Additionally, precise reproductive synchronization may not be an adaptive mechanism in temporally unpredictable large river environments. Similar protracted spawning windows have been observed for other large river fishes along regulated river systems, perhaps either as adaptive responses or as interruptions of spawning activity under such manipulated river conditions (June 1977; McCabe and Tracy 1994).

Variability in the inter-annual distribution of last contact dates could have been the result of yearly differences in seasonal river temperatures or the maturation status of tagged fish. Because temperature plays a role in regulating the rates of final maturation in fish (Bye 1984; Stacey 1984; Jobling 1995), the cold May temperatures in 2002 may have delayed the timing of spawning in many of the fish that remained in the river for an extended period of time that year. Additionally, males that exited early throughout the study may have not been capable of spawning. The lack of upriver movement displayed by these fish was consistent with that reported in individuals that were in between spawns in other paddlefish populations (Filipek 1990). Though gonadal samples from paddlefish harvested in North Dakota and Montana during the spring have indicated that over 96% of males were capable of spawning (unpublished data from this study), uncertainty exists for the tagged males in this study because they were not staged.

The extent of the fish migration in this study, in terms of aggregate distances moved upriver by tagged fish, was not found to be significantly greater in the higher flow year of 1999 (peak discharge 1509 m^3/s on June 26) than the lower flow year of 2001 (peak discharge 680 m^3/s on June 17). Other studies, however, have found a positive association between the magnitude and duration of high spring flows and the number of paddlefish participating in the spawning migration (Rehwinkel 1978; Lein and DeVries 1998; Paukert and Fisher 2001). Fluctuating discharge has been implicated in the premature termination of the spawning migration in other large-river migratory fish as well (Paragamian and Kruse 2001). Conversely, low flows may influence the extent rather than the strength of the paddlefish migration by inhibiting persistent upriver movement (Elser 1977; Purkett 1961). Purkett (1961), not finding female paddlefish at upriver sites during a year of fluctuating spring discharge along the Osage River, Missouri, suggested that fish may have spawned in reaches downriver.

Results of the snag fishery at Intake indicated that more fish were present at Intake in 1999 (1706 harvested fish) than in 2001 (360 harvested fish), yet among tagged fish movement to Intake was comparable in the two years. At least two factors may have contributed to this discrepancy; effects of tag implantation on behavior, and the tagging of a non-random sample of the migratory fish. Because fish were tagged in late April of 1999 immediately prior to the initial rise in YR discharge, stress incurred during the surgery could have suppressed the upriver response to increasing flows. Unexpected downriver movements have been noted in other large-river migratory fishes after excessive handling during tagging (Hall et al. 1991; Moser and Ross 1995). Alternatively, the sample of tagged fish may not have been representative of the entire migratory segment of the population. Tagging efforts were biased toward fish that staged in reaches along the MRBC. Other overwintering sites not targeted in this study may have harbored paddlefish that had different migratory tendencies. Associations between overwintering reaches and pre-spawning migration patterns have been documented in populations of shortnose sturgeon, *Acipenser brevirostrum* (Buckley and Kynard 1985; Kynard 1997).

Evidence of different migratory tendencies among individual paddlefish was indicated by the consistent behaviors observed within repeat migrants. Many tagged fish either made only modest forays up the river system (fishes 251, 311, 691, 801, and 900), or terminated their upriver movement along the same stretch of the lower 50 rkm of the YR (fishes 492, 591, 741, 821, 841, and 910) in each of the springs in which they migrated. Furthermore, though some fish ascended above MRkm 70 during small rises in MR discharge, these same fish were not found to move above YRkm 50 during much greater increases in YR discharge (fishes 641, 821, and 611; Table 7). One male (fish 571), however, was repeatedly contacted in reaches below Intake in both higher and lower flow years. These results indicate that some fish may be inclined to migrate to certain reaches of the YR regardless of river conditions during the spring.

The apparent site fidelity exhibited by repeat migrants in this study can be discussed in the context of individual proclivities for moving certain distances upriver during the spawning migration. Fish may restrict the extent of their migration to river reaches attended to in previous spawning runs (Lucas and Baras 2001). Such behavior, suggestive of reproductive homing instincts, has been reported in populations of both paddlefish (Stancill et al. 2002) and sturgeon (Wooley and Crateau 1985; Foster and Clugston 1997; Heise et al. 2004). Equally important in determining expressed migratory behaviors may be the presence of unique bioenergetic attributes that facilitate long, exploratory movements (Secor 1999), or the inheritance of 'hard-wired' instructions for traveling specific distances during upriver migrations (McIsaac and Quinn 1988). Harvest data from this population has revealed a higher percentage of young mature paddlefish in the Intake than in the Confluence fishery (D. Scarnecchia, University of

Idaho, pers. comm.). Although not exhaustive of all possibilities, the difference in the age structure between the two fisheries could be the result of separate sub-stocks with different genetically-determined, migratory patterns and exploitation rates, or evidence of energetic differences in young paddlefish that facilitate exploratory migrations up the YR.

Paddlefish that were contacted in more than one year also provided information on migratory periodicity within this population. The presence of tagged females in the river every 2 or 3 years, but not in consecutive years, is consistent with that reported by Russell (1986). Males, on the other hand, were often contacted every other year or in successive migrations during our study. Although male paddlefish are considered to be capable of spawning annually in some river systems (Russell 1986), it is not known whether the males that had migrated in 2001 and 2002 actually spawned in either year. River conditions during the low flow year of 2001 may have not provided the cues necessary to induce spawning in these males, especially in the fish that was contacted at Intake in both springs. Due to energetic expenditures, long distance migrations and annual spawning may not be compatible reproductive tactics in male paddlefish as has been suggested for male shortnose sturgeon (Kieffer and Kynard 1996).

Although this study provided information as to how paddlefish respond to variable river conditions during their spawning migration, more information is needed on the link between migratory behavior and spawning success. Inter-annual differences in spring discharge, though seemingly not influencing the spatial or temporal aspects of migratory behavior, may have a pronounced influence on spawning cues. In addition, it is not yet known if there is differential reproductive success in fish migrating to different stretches of the lower Yellowstone River. Different migratory types may be associated with age or physiological condition which, in turn, could affect egg or larval quality. Furthermore, characteristic features of suitable paddlefish spawning habitat are more abundant along reaches below Intake than along the lower 50 rkm of the Yellowstone River where fish were typically distributed throughout the migration. Until more is known about the adaptive significance of variable spawning tactics of individual paddlefish, it is important to maintain the diversity of behaviors apparent within this population.

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Table 1. Statistics for the YR flow and thermal regimes for 1999-2002. For each year, the YR flow regime was separated into two periods: an initial period of fluctuating, slowly increasing discharge (Before), and a latter period of rapidly increasing discharge (After). Degree days were calculated by summing daily mean temperatures above 0°C.

	Flow Regime			**Thermal regime**	
Year	Time Period	Peak discharge (m^3/s)	Peak suspended sediment (mg/L)	May Degree Days	June Degree Days
1999	Before May 23	544	3670	446	542
	After May 23	1509	2440		
2000	Before May 20	365	853	501	556
	After May 20	997	3110		
2001	Before May 27	569	1600	517	586
	After May 27	680	4100		
2002	Before May 18	223	1980	408	585
	After May 18	1093	3320		

Table 2. Summary statistics of radio-tagged paddlefish in the Yellowstone and Missouri Rivers, 1999-2002.

Fish[a]	Date Tagged	Length (cm)	Weight (kg)	Sex	Number of Contacts[b]	Days at Large[c]	Fate[d]
461	04/30/99	104	24.5	F	10	80	
471	04/30/99	117	28.8	F	1(3)	125	Expelled tag at MRkm -6.5 on 9/2/99
481	04/30/99	112	29.3	F	4(8)	63	Expelled tag recovered in reservoir on 7/2/99
355	04/30/99	119	29.9	F	10	42	
492	04/30/99	114	30.6	F	20	1158	
551	04/30/99	112	30.8	F	3	33	
511	04/30/99	119	32.2	F	7	117	
372	04/29/99	124	34.5	F	3(13)	19	Expelled tag atYRkm 14.5 on 5/18/99
394	04/30/99	119	34.5	F	7	42	
541	04/30/99	119	37.1	F	11	53	
501	04/30/99	117	37.6	F	2	7	Harvested at confluence on 5/7/99
561	04/29/99	127	42.6	F	0(4)	54	Expelled tag at MRkm -27 on 6/22/99
581	04/29/99	89	10.9	M	15	1134	
451	04/30/99	94	12.2	M	9	1158	
601	04/29/99	89	12.9	M	24	1245	
421	04/30/99	94	12.9	M	2(5)	42	Expelled tag atYRkm 35 on 6/11/99
401	04/30/99	91	13.2	M	3	42	
591	04/29/99	91	14.1	M	30	1159	
441	04/30/99	97	15.4	M	0(5)	50	Expelled tag at MRkm -3.5 on 6/19/99
411	04/30/99	94	15.9	M	8	132	
621	04/29/99	104	16.8	M	36	784	
611	04/29/99	102	16.9	M	22	1159	
571	04/29/99	102	18.4	M	52	1146	
531	04/29/99	107	19.5	M	11(8)	43	Expelled tag at YRkm 30 on 6/11/99
521	04/29/99	102	20.4	M	23	744	Harvested at MRkm -32 on 5/12/01
721	09/30/99	112	19.1	F	36	978	
821	09/30/99	104	24	F	34	1104	
681	10/05/99	109	27.2	F	23	246	
501[e]	10/05/99	119	29.5	F	18	279	
870	10/05/99	122	32.7	F	11	987	
431	10/05/99	122	33.1	F	17	231	
910	10/05/99	124	33.6	F	24	973	
701	10/05/99	119	34.5	F	42	973	
691	09/30/99	122	39.5	F	34	972	
860	09/30/99	89	10	M	9(20)	174	Expelled tag at MRkm -35 on 3/22/00
651	09/30/99	91	10.9	M	9(18)	182	Expelled tag at MRkm -16 on 3/30/00
711	09/30/99	86	12.2	M	0(28)	7	Expelled tag at MRkm -16 on 10/7/99
801	09/30/99	99	14.5	M	37	944	
641	09/30/99	99	15	M	28	986	
900	09/30/99	97	15	M	59	1104	
890	10/05/99	107	16.8	M	24	1156	
741	09/30/99	104	17.2	M	47	998	
671	10/05/99	104	18.6	M	18	221	Harvested at MRkm -14.5 on 5/13/00
661	09/30/99	107	19.5	M	34	1104	
730	10/05/99	107	19.5	M	21	955	
780	09/30/99	109	20.9	U	35	726	
841	09/30/99	104	20.9	U	42	1104	

Table 2 (continued). Summary statistics of radio-tagged paddlefish in the Yellowstone and Missouri Rivers, 1999-2002.

Tag[a]	Date Tagged	Length (cm)	Weight (kg)	Sex	Number of Contacts[b]	Days at Large[c]	Fate[d]
271	09/28/00	112	24.0	F	9	246	
091	09/27/00	102	25.9	F	16(10)	226	Expelled tag at YRkm 22.5 on 5/11/01
331	09/28/00	112	28.1	F	14	251	
051	09/27/00	112	29.0	F	14	255	
171	09/27/00	117	30.8	F	21	257	
481[e]	09/28/00	114	32.2	F	5	32	
191	09/27/00	119	32.7	F	14	247	
151	09/27/00	119	33.1	F	19	252	
031	09/27/00	119	34.5	F	20	267	
864	09/28/00	114	34.5	F	7	246	
071	09/27/00	99	14.1	M	16	227	Harvested at YRkm 14.5 on 5/12/01
131	09/27/00	97	14.1	M	16	684	
311	09/28/00	94	14.1	M	33	797	
251	09/28/00	99	14.5	M	22	580	
671[e]	09/28/00	99	14.5	M	18	797	
011	09/27/00	99	15.9	M	14	220	
231	09/27/00	99	15.9	M	11	226	
930	09/28/00	107	17.7	M	22	740	
211	09/27/00	102	19.5	M	39	741	
881	09/28/00	104	19.5	M	20	618	Harvested at YRkm 110 on 6/8/02
111	09/27/00	107	20.9	M	10	219	Harvested at MRkm -6.5 on 5/4/01
291	09/28/00	97	20.9	U	0		

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[a] Fish that were contacted in more than one spring migration are in bold

[b] Number of contacts after presumed expulsion is given in parentheses

[c] Number of days between last contact, harvest, or tag expulsion and tagging date

[d] Dates provided for expelled tags indicate when tags were first found to be stationary

[e] Tag was re-implanted from a previously tagged fish that was harvested or had expelled its tag

Table 3. Summary length and weight statistics for radio-tagged paddlefish. Mean values are given in parentheses.

Sex	Tagging Period	Number	Length range (cm)	Weight range (kg)
F	S99	12	104-127 (117)	24.5-42.6 (32.7)
	F99	9	104-124 (117)	19.1-39.5 (30.4)
	F00	10	102-119 (114)	24.0-34.5 (30.5)
	Total	**31**	**102-127 (116)**	**19.1-42.6 (31.3)**
M	S99	13	89-107 (97)	10.9-20.4 (15.3)
	F99	11	86-107 (99)	10.0-19.5 (15.4)
	F00	11	94-107 (101)	14.1-20.9 (16.4)
	Total	**35**	**86-107 (98)**	**10.0-20.9 (15.7)**
U	F99	2	104-109 (107)	20.9
	F00	1	97	20.9
	Total	**3**	**97-109 (103)**	**20.9**

Table 4. Summary of spring movement statistics for radio-tagged paddlefish in the Yellowstone and Missouri Rivers, 1999.

Fish	Sex	Number of Contacts	Date First Contacted Above Confluence	Number of Times Moved Above Confluence	Furthest rkm up YR	Furthest rkm up MRAC
372[a]	F	3	5/12	1	25.4	
394	F	7	5/12	3	24.9	38.9
531[a]	M	11	5/12	1	38.8	
571	M	13	5/12	1	109.3	
581	M	3	5/12	1	36.6	
451	M	4	5/13	1	15	
492	F	11	5/13	2	40.6	
541	F	11	5/14	1	32	
461	F	7	5/17	1	96.1	
601	M	4	5/17	1	48	
611	M	6	5/17	2	14.5	
521	M	7	5/19	2	31.8	
551	F	3	5/20	1	9.2	
355	F	10	5/24	2	20.9	0.4
591	M	10	5/24	1	53.4	
401	M	3	5/27	1	33.4	
621	M	9	5/27	1	77.6	
411	M	3	5/31	1	111.3	
421[a]	M	2	6/2	1	45.6	
481[a]	F	4	6/11	1	8.1	
471[a]	F	1	---	0		
501[b]	F	2	---	0		
511	F	1	---	0		

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[a] Tag presumed expelled

[b] Fish harvested

Table 5. Summary of spring movement statistics for radio-tagged paddlefish in the Yellowstone and Missouri Rivers, 2000.

Fish	Sex	Number of Contacts	Date First Contacted Above Confluence	Number of Times Moved Above Confluence	Furthest rkm up YR	Furthest rkm up MRAC
741	M	19	5/1	3	40.6	4.5
841	U	19	5/1	1	40.9	
821	F	11	5/2	3	33.8	4.3
730	M	14	5/5	3	28.2	4
910	F	12	5/6	2	30.7	
701	F	23	5/8	3	71.8	
780	U	20	5/15	3	27.8	
721	F	19	5/24	1	41	
691	F	10	5/25	1	13.2	
900	M	14	5/25	2	10.5	
870	F	10	5/27	1	25.4	
661	M	6	6/3	1		198
501	F	7	---	0		
431	F	6	---	0		
641	M	4	---	0		
651[a]	M	1	---	0		
671[b]	M	7	---	0		
681	F	12	---	0		
801	M	6	---	0		
890	M	6	---	0		

[a] Tag presumed expelled

[b] Fish harvested

Table 6. Summary of spring movement statistics for radio-tagged paddlefish in the Yellowstone and Missouri Rivers, 2001.

Fish	Sex	Number of Contacts	Date First Contacted Above Confluence	Number of Times Moved Above Confluence	Furthest rkm up YR	Furthest rkm up MRAC
231	M	6	4/25	2	29.9	1.8
071[b]	M	8	5/5	1	19.6	
131	M	5	5/5	1		2.4
191	F	11	5/5	4	30.7	1.0
251	M	5	5/5	1		0.5
331	F	9	5/5	3	44.7	
671	M	11	5/5	4	21.6	3.5
091[a]	F	6	5/8	1	23.0	
571	M	10	5/8	2	111.2	
591	M	10	5/8	3	51.2	
864	F	7	5/8	3	28.6	
151	F	11	5/16	2	24.8	
051	F	11	5/18	2	87.9	
171	F	16	5/18	3	13.4	1.1
621	M	11	5/18	1	35.9	
271	F	6	5/19	2	26.9	
601	M	10	5/19	3	36.9	
031	F	11	5/23	2	42.5	
211	M	11	5/23	2	11.6	
311	M	8	5/23	1	1.1	
881	M	5	5/23	1	35.2	
900	M	7	5/23	1	1.1	
930	M	13	5/23	1	42.6	
011	M	5	--	0		
111[b]	M	4	--	0		
521[b]	M	7	--	0		

[a] Tag presumed expelled

[b] Fish harvested

Table 7. Summary of spring movement statistics for radio-tagged paddlefish in the Yellowstone and Missouri Rivers, 2002.

Fish	Sex	Number of Contacts	Date First Contacted Above Confluence	Number of Times Moved Above Confluence	Furthest rkm up YR	Furthest rkm up MRAC
641	M	7	4/23	3	34.1	99.5
841	U	7	4/23	1	47.8	
701	F	6	5/11	2	28.5	
571	M	8	5/14	2	100.4	0.6
691	F	6	5/14	2	5.6	17.4
721	F	3	5/14	2	15.6	0.5
730	M	4	5/14	1		60.5
821	F	4	5/14	2	27.7	96.1
881[a]	M	5	5/14	2	103.0	4.8
211	M	4	5/16	1		19.6
581	M	7	5/16	2	14.2	2.6
611	M	8	5/17	3	47.5	73.2
741	M	10	5/21	2	32.5	
910	F	4	5/21	2	33.0	
451	M	3	5/29	1	37.8	
900	M	4	5/29	1	2.4	
492	F	5	6/4	1	35.2	
591	M	8	6/4	1	53.4	
870	F	1	6/18	1	9.7	
251	M	2	--	0		
311	M	3	--	0		
801	M	2	--	0		

[a] Fish harvested

Table 8. Results of model selection analysis for the regression of radio-tagged paddlefish movements on various subsets of explanatory variables during the springs of 2000 and 2001. The explanatory variables, Prin1, Prin2, and Prin3, represent the three principal components created from the PCA conducted on the original variables (see Table 9). A model with an AIC$_i$ difference ≤ 2 was considered in the subset of best approximating model, whereas a model with an AIC$_i$ difference > 10 was considered to have no support as the best model and was not used in the calculation of Akaike weights (w_i's). The relative importance of each of the principal components is provided at the bottom of the table.

Year	**Model**	**Number of parameters**[a]	**AIC$_i$ difference**	**w_i**
2000	Prin1	3	0.00	0.44
	Prin1, Prin3	4	0.89	0.28
	Prin1, Prin2	4	1.82	0.18
	Prin1, Prin2, Prin3	5	2.83	0.11
	No explanatory variables	2	34.80	---
	Prin3	3	35.40	---
	Prin2	3	36.88	---
	Prin2, Prin3	4	37.57	---
2001	Prin1, Prin2, Prin3	5	0.00	0.76
	Prin1, Prin3	4	2.26	0.24
	Prin1, Prin2	4	19.74	---
	Prin1	3	20.08	---
	Prin2, Prin3	4	30.87	---
	Prin3	3	32.93	---
	Prin2	3	42.31	---
	No explanatory variables	2	42.95	---

	Explanatory variable	**Coefficient sign**	**Relative importance**[b]
2000	Prin1	Positive	1.00
	Prin3	Negative	0.39
	Prin2	Positive	0.28
2001	Prin1	Positive	1.00
	Prin3	Negative	1.00
	Prin2	Positive	0.76

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[a] Parameters included explanatory variables, intercept, and variance term

[b] Calculated by summing up the w_i's of each model that contained that explanatory variable

Table 9. Summary statistics from the PCA on the three river variables, change in discharge, change in suspended sediment, and change in temperature for the springs of 2000 and 2001.

			Component correlation vector[a]		
Year	**Principal components**	**Percent variation explained by component**	Change in discharge	Change in suspended sediment	Change in temperature
2000					
	Prin1	62	0.90	0.88	-0.50
	Prin2	28	0.20	0.29	0.85
	Prin3	10	0.39	-0.37	0.03
2001					
	Prin1	66	0.91	0.97	-0.43
	Prin2	31	0.34	0.07	0.90
	Prin3	3	-0.21	0.23	0.06

[a] Correlation between the principal component and the original variables listed below

Table 10. Results of model selection analysis for the logistic regression of radio-tagged paddlefish river selection on various subsets of predictor variables during the springs of 2000-2002. The predictor variables, Prin1, Prin2, and Prin3, represent the three principal components created from the PCA conducted on the original variables (see Table 11). A model with an AIC_i difference ≤ 2 was considered in the subset of best approximating model, whereas a model with an AIC_i difference > 10 was considered to have no support as the best model and was not used in the calculation of Akaike weights (w_i's). The relative importance of each of the principal components is provided at the bottom of the table.

Model	Number of parameters[a]	AIC_i difference	w_i
Prin1	2	0.00	0.56
Prin1, Prin3	3	2.09	0.20
Prin1, Prin2	3	2.21	0.19
Prin1, Prin2, Prin3	4	4.52	0.06
No predictor variables	1	10.71	---
Prin3	2	12.81	---
Prin2	2	12.95	---
Prin2, Prin3	3	15.27	---

Predictor variable	Coefficient sign	Relative importance[b]
Prin1	Positive	1.00
Prin3	Positive	0.26
Prin2	Negative	0.24

---

[a] Parameters included the predictor variables and the intercept

[b] Calculated by summing up the w_i's of each model that contained that predictor variable

Table 11. Summary statistics from the PCA on the three variables, rate of change in discharge difference, average turbidity difference, and average discharge difference calculated from data collected during periods when radio-tagged paddlefish ascended the Confluence during 2000-2002 (see text for description of variables).

		Component correlation vector[a]		
Principal components	**Percent variation explained by component**	Rate of change in discharge difference	Average turbidity difference	Average discharge difference
Prin1	74	0.77	0.91	0.88
Prin2	18	0.62	-0.19	-0.36
Prin3	8	0.07	-0.39	0.31

[a] Correlation between the component and the original variables listed below

Table 12. Aggregations of two or more radio-tagged paddlefish during spring survey dates, 1999-2002. In each case, at least one of the individuals was contacted for the last time during the spring indicating potential spawning locations along the respective reach. Rkm indicated the mid-point of the reach where paddlefish were contacted, and positive and negative values indicate the number of river kilometers up the YR or below the Confluence, respectively.

Year	Date	Rkm	Length of reach	Number of fish in aggregation[a]
1999	5/19	37.0	0.9	2M
	6/11	21.0	0.3	2F
	6/11	46.3	1.0	2M
	6/22	0.1	0.6	1F,1M
2000	5/2	-22.1	0.2	1F,1M
	6/6	5.6	0.5	2M
	6/22	28.6	0.1	2F,1M
	7/5	36.0	0.1	1F,1U
2001	5/23	1.1	0.1	2M
	5/23	35.2	0.1	1F,1M
	6/1	21.6	0.1	2M
	6/11	0.0	0.1	1F,1M
2002	5/1	-13.4	0.3	3M
	5/7	-13.2	0.5	3M
	5/29	0.0	0.1	2F
	5/29	2.4	0.1	2M
	6/4	32.8	0.5	1F,1M

[a] F, M, U refers to female, male, and unknown sex, respectively

Table 13. Comparisons of the furthest river kilometers attained by radio-tagged paddlefish that were contacted in at least two of the four spring migrations during 1999-2002. Positive and negative values indicate the number of river kilometers above and below the Confluence, respectively.

	Tagging		Furthest Contact up River System (rkm)			
Fish	Period	Sex	1999	2000	2001	2002
611	S99	M	14.5			47.5
451	S99	M	15.0			37.8
521	S99	M	31.8		0[a]	
581	S99	M	36.6			14.2
601	S99	M	48.0		36.9	
591	S99	M	53.4		51.2	53.4
621	S99	M	77.6		35.9	
571	S99	M	109.3		111.2	100.4
492	S99	F	40.6			35.2
841	F99	U		40.9		47.8
641	F99	M		-11.4		34.1
801	F99	M		-6.1[b]		-13.2[b]
900	F99	M		10.5	1.1	2.4
730	F99	M		28.2		60.5[c]
741	F99	M		40.6		32.5
691	F99	F		13.2		5.6
870	F99	F		25.4		9.7
910	F99	F		30.7		33.0
821	F99	F		33.8		27.7
721	F99	F		41.0		15.6
701	F99	F		71.8		28.5
251	F00	M			0.5[b,c]	-13.2[b]
311	F00	M			1.1	-13.4
211	F00	M			11.6	19.6[c]
881	F00	M			35.2	103.0

[a] Harvested on May 12

[b] Last contacted in first week in May

[c] Indicates furthest contact up MRAC because fish was not contacted up YR

Figure 1. Map of the study area

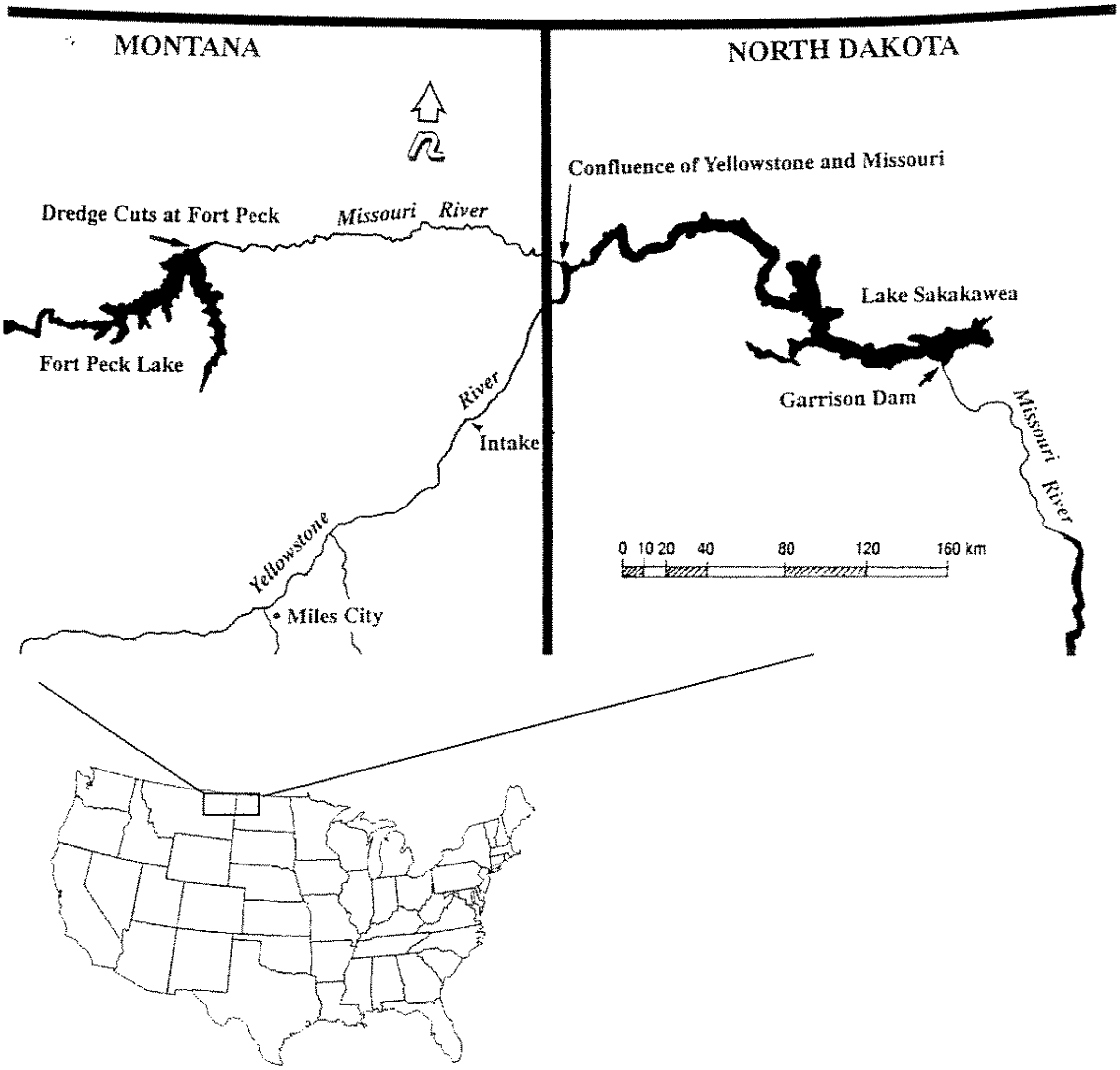


Figure 2. Yellowstone River (YR) and the Missouri River (MRAC) discharge and thermal regimes from April 20 to July 15 of 1999-2002.

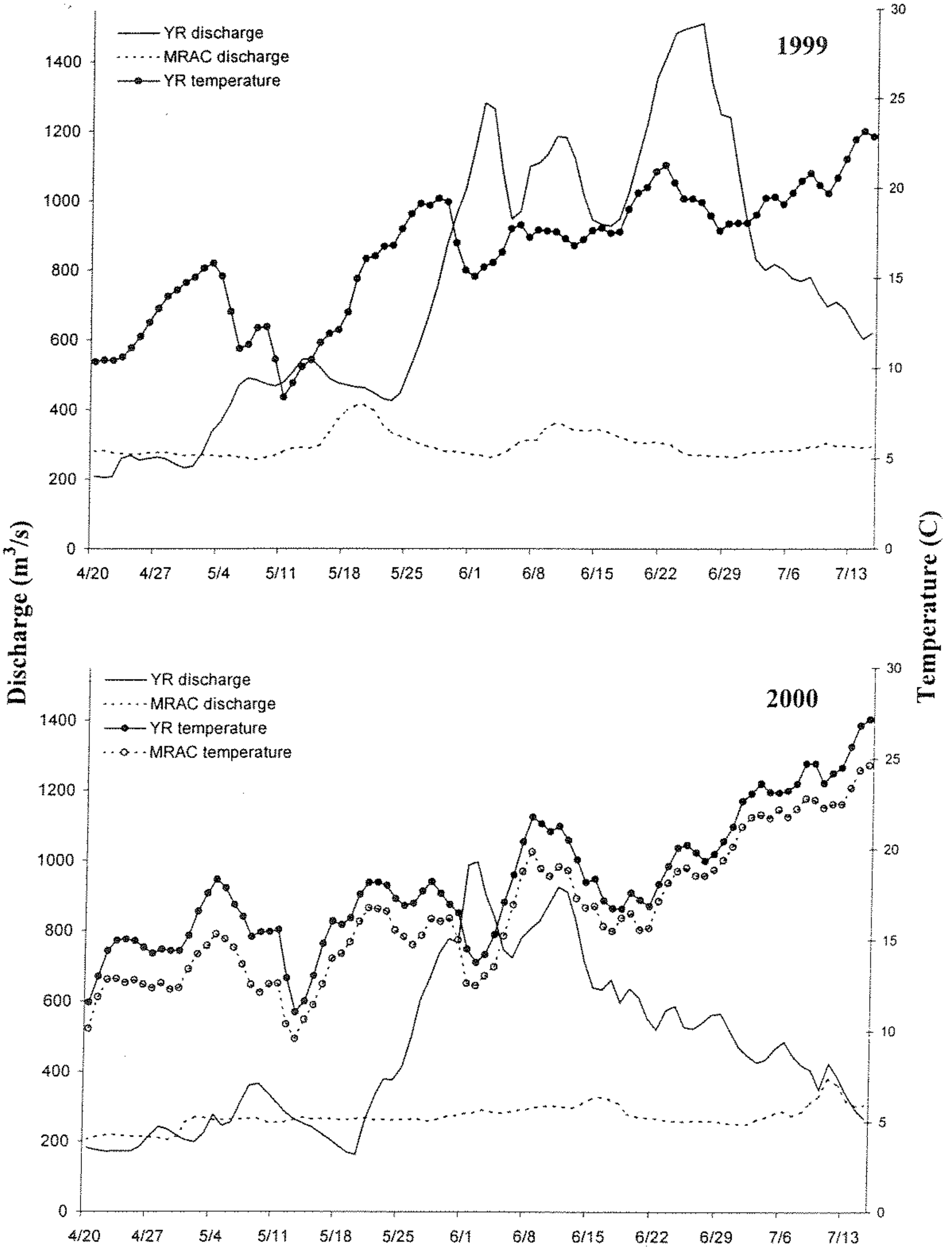


Figure 2 (continued). Yellowstone River (YR) and the Missouri River (MRAC) discharge and thermal regimes from April 20 to July 15 of 1999-2002.

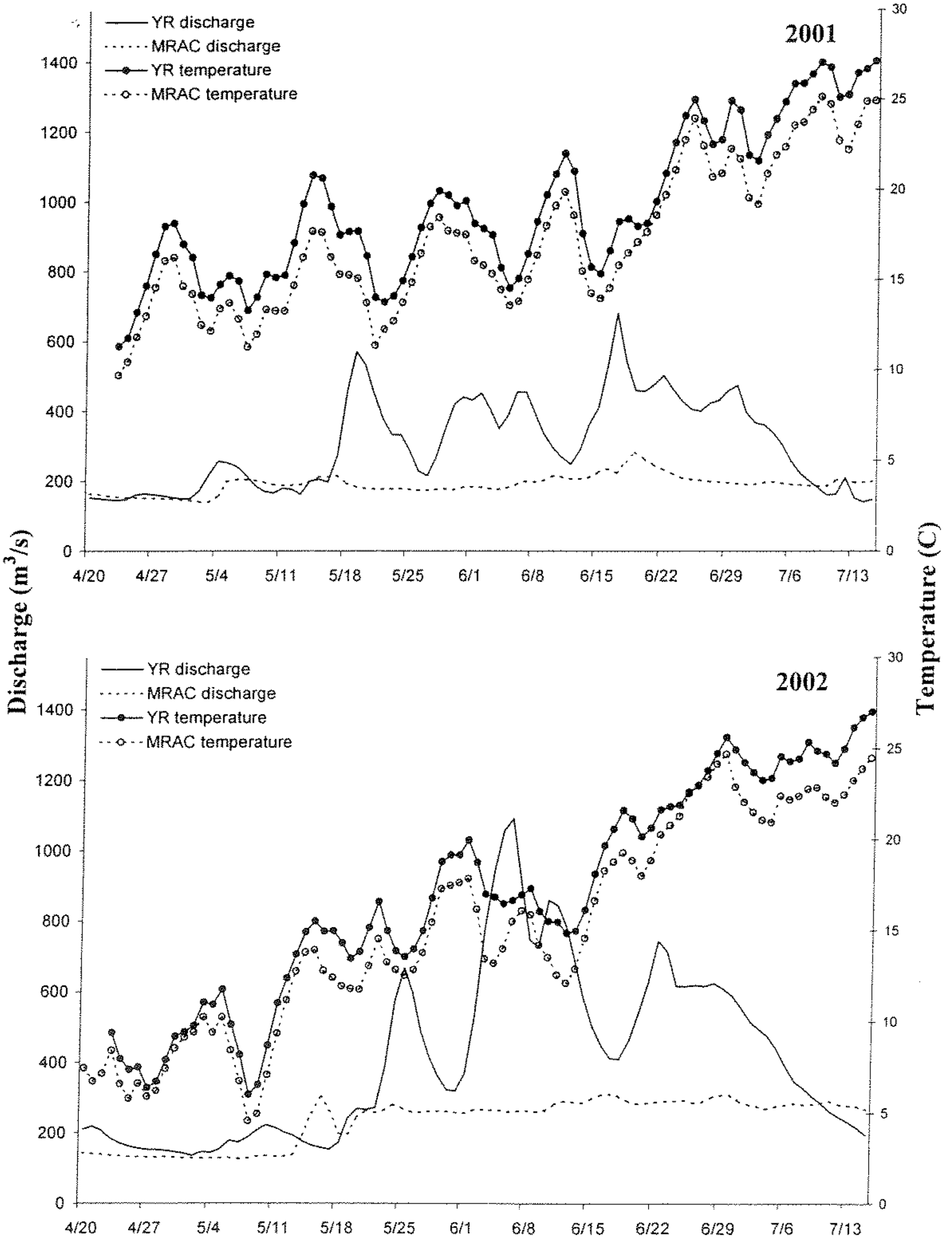


Figure 3. Distribution of radio-tagged paddlefish contacts (May 2-June 29) along the YR and MR in relation to YR discharge, suspended sediment, and temperature during the spring of 1999. Positive and negative river kilometer (rkm) indicates the number of kilometers above and below the Confluence, respectively. The solid horizontal line represents the Confluence, whereas the vertical dotted line separates the two discharge periods (see Table 1).

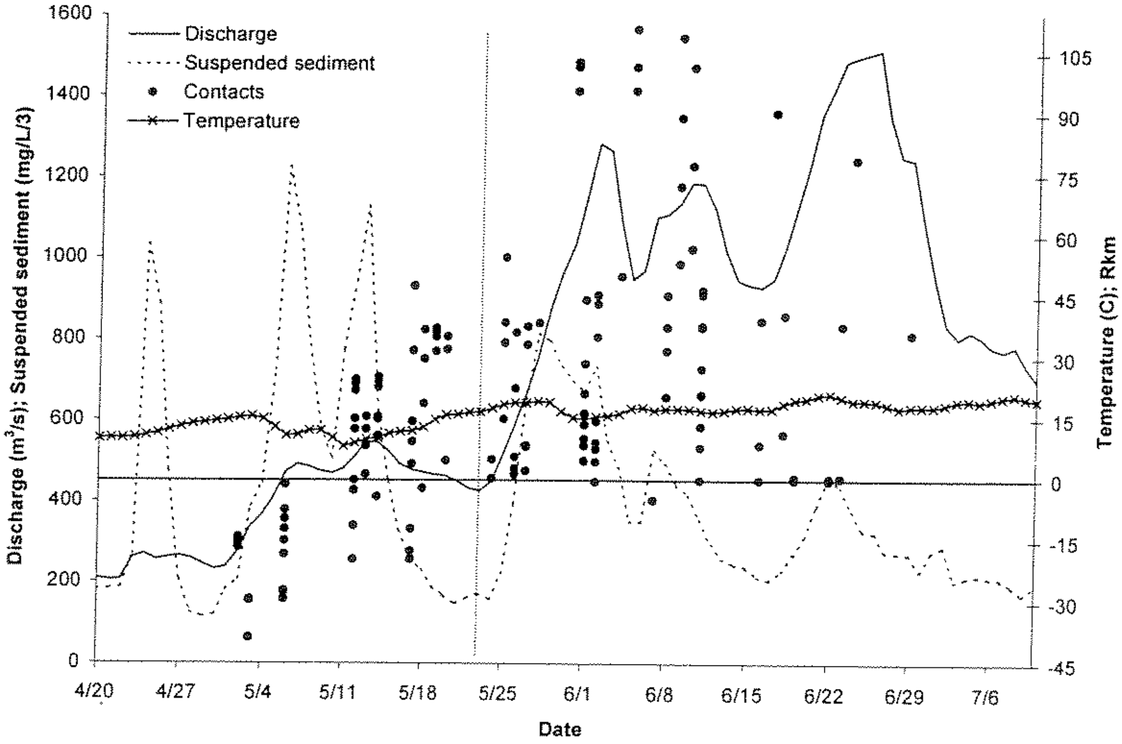


Figure 4. Distribution of radio-tagged paddlefish contacts (March 22-July 5) along the YR and MR in relation to YR discharge, suspended sediment, and temperature during the spring of 2000. Positive and negative river kilometer (rkm) indicates the number of kilometers above and below the Confluence, respectively. One fish was contacted 198 rkm above the Confluence along the MR (not displayed). The solid horizontal line represents the Confluence, whereas the vertical dotted line separates the two discharge periods (see Table 1).

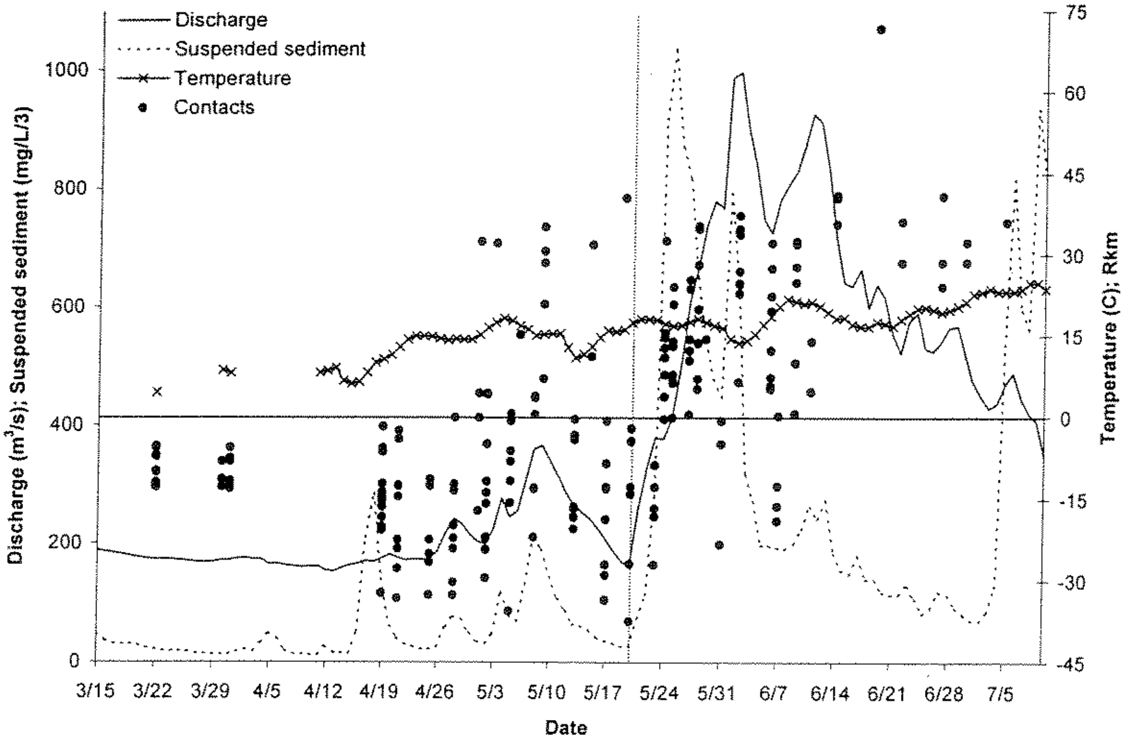


Figure 5. Distribution of radio-tagged paddlefish contacts (April 19 – June 21) along the YR and MR in relation to YR discharge, suspended sediment, and temperature during the spring of 2001. Positive and negative river kilometer (rkm) indicates the number of kilometers above and below the Confluence, respectively. The solid horizontal line represents the Confluence, whereas the vertical dotted line separates the two discharge periods (see Table 1).

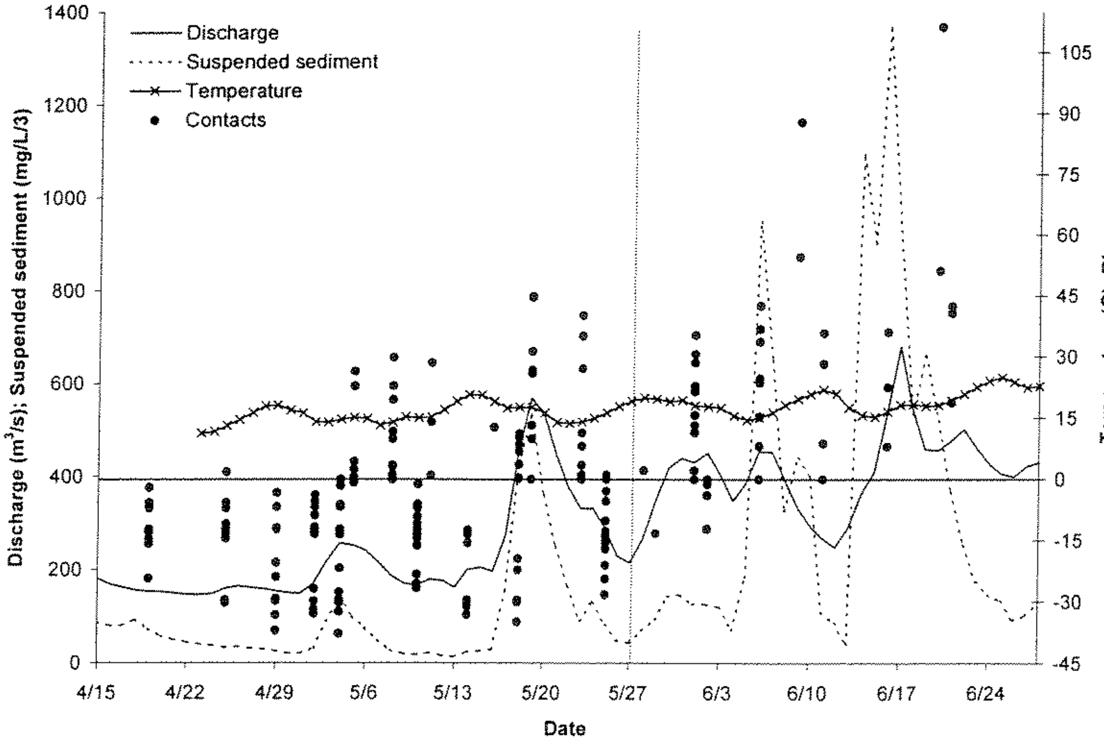


Figure 6. Distribution of radio-tagged paddlefish contacts (April 23 – July 1) along the YR and MR in relation to YR discharge, suspended sediment, and temperature during the spring of 2002. Positive and negative river kilometer (rkm) indicates the number of kilometers above and below the Confluence, respectively. Open circles indicate rkm above the Confluence along the MR where paddlefish were aerially contacted. The solid horizontal line represents the Confluence, whereas the vertical dotted line separates the two discharge periods (see Table 1).

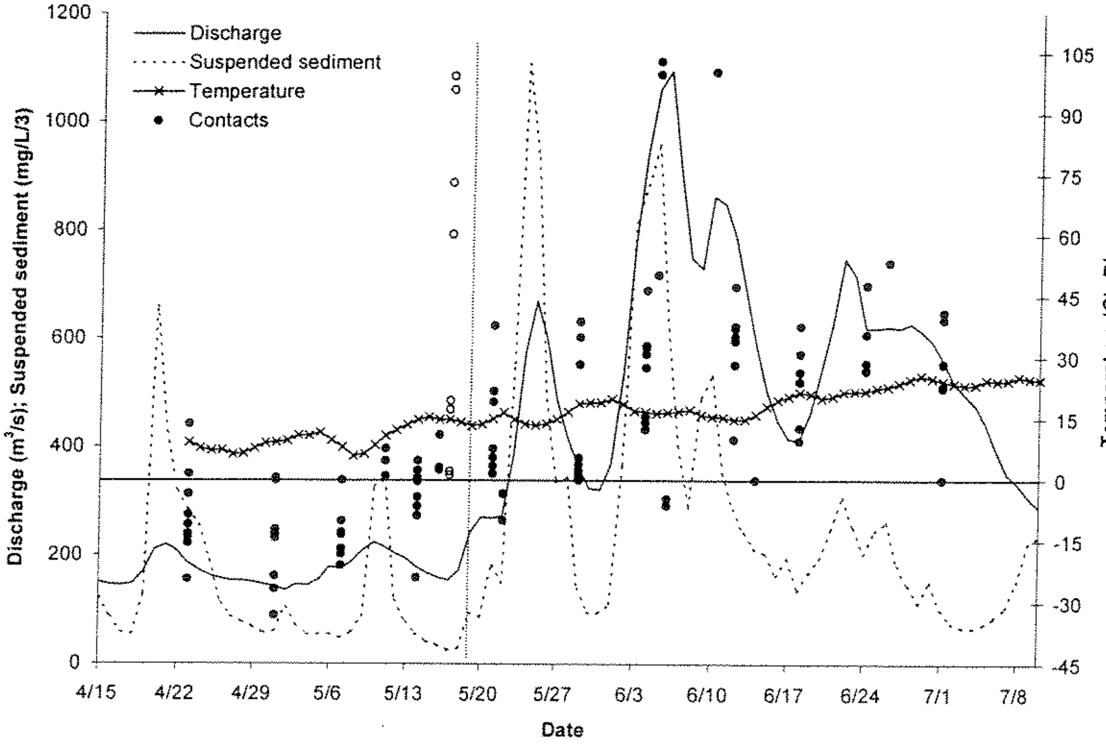


Figure 7. Comparison of individual radio-tagged paddlefish upriver movement rates between different periods of increasing discharge for 2000 (n=9) and 2001 (n=9). Each individual is represented by a pair of vertical bars. For 2000, periods one and two correspond to the gradual rise in discharge (187-365 m^3/s) that occurred from April 26 to May 9 and the rapid rise in discharge (163-997 m^3/s) that occurred from May 20 to June 2, respectively. For 2001, periods one and two correspond to the gradual rise in discharge (150-240 m^3/s) that occurred from May 1 to May 6 and the rapid rise in discharge (200-570 m^3/s) that occurred from May 14 to May 19, respectively. An asterisk next to the year indicates that movement rates were significantly different ($p<.01$) between discharge periods.

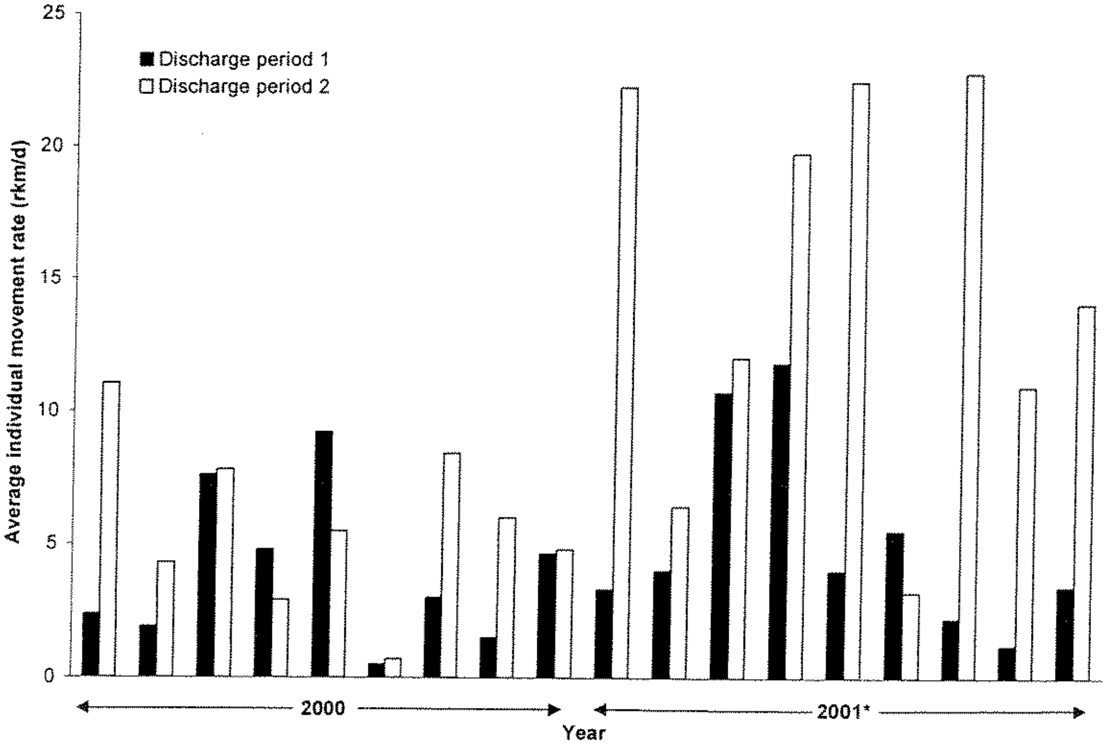


Figure 8. Paddlefish movement rates in relation to the number of elapsed days between contacts.

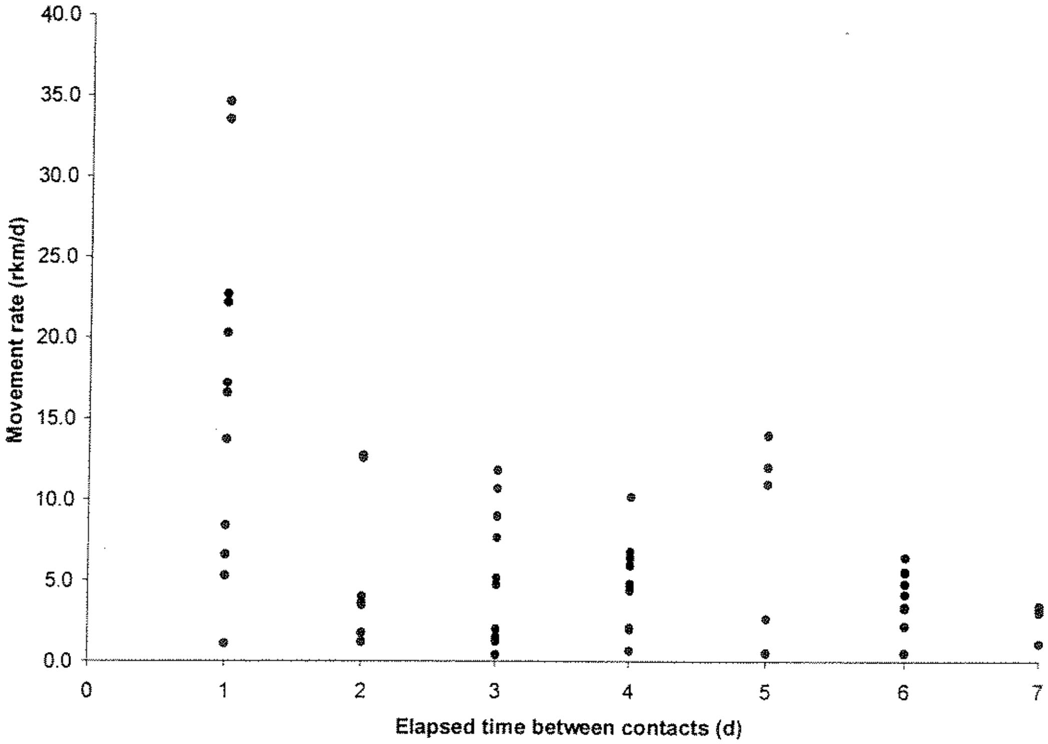


Figure 9. The cumulative number of river kilometers (rkm) traversed by female (F) and male (M) radio-tagged paddlefish during 2000 and 2001. Horizontal dash indicates the mean level for each distribution.

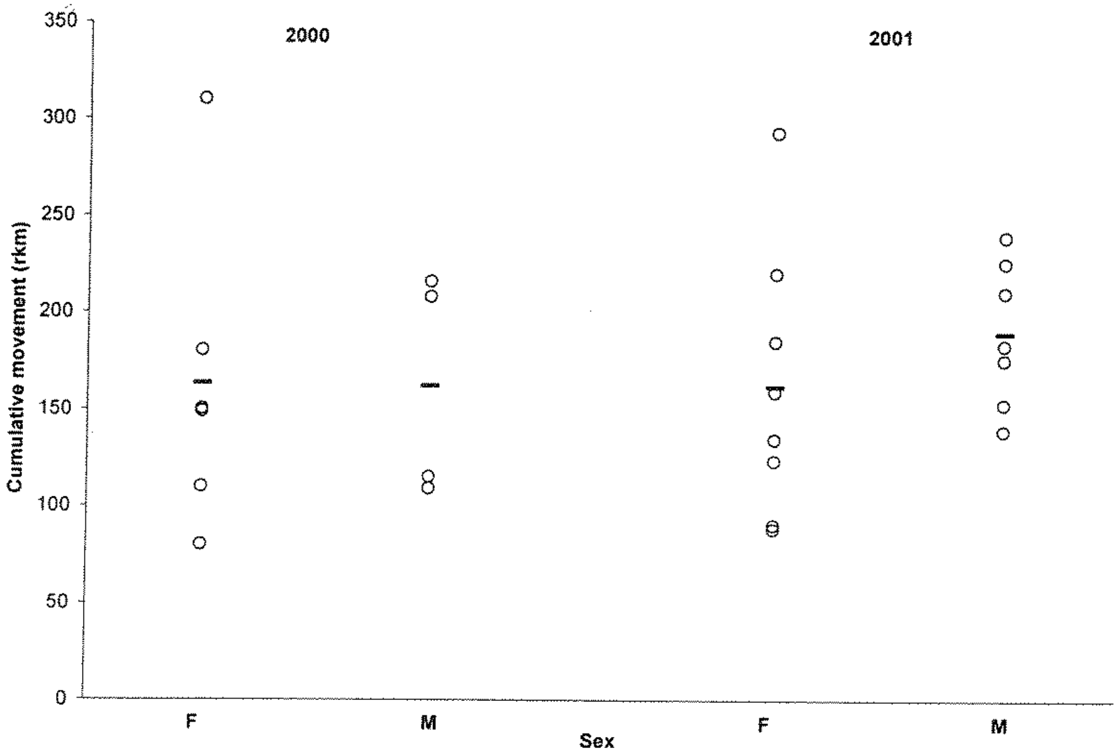


Figure 10. Comparison of river discharge and turbidity in the YR and MRAC during the time period in which radio-tagged paddlefish were contacted in the MRAC in 1999. Arrows indicate when fish were contacted in the MRAC after a previous contact either in the MRBC or the YR.

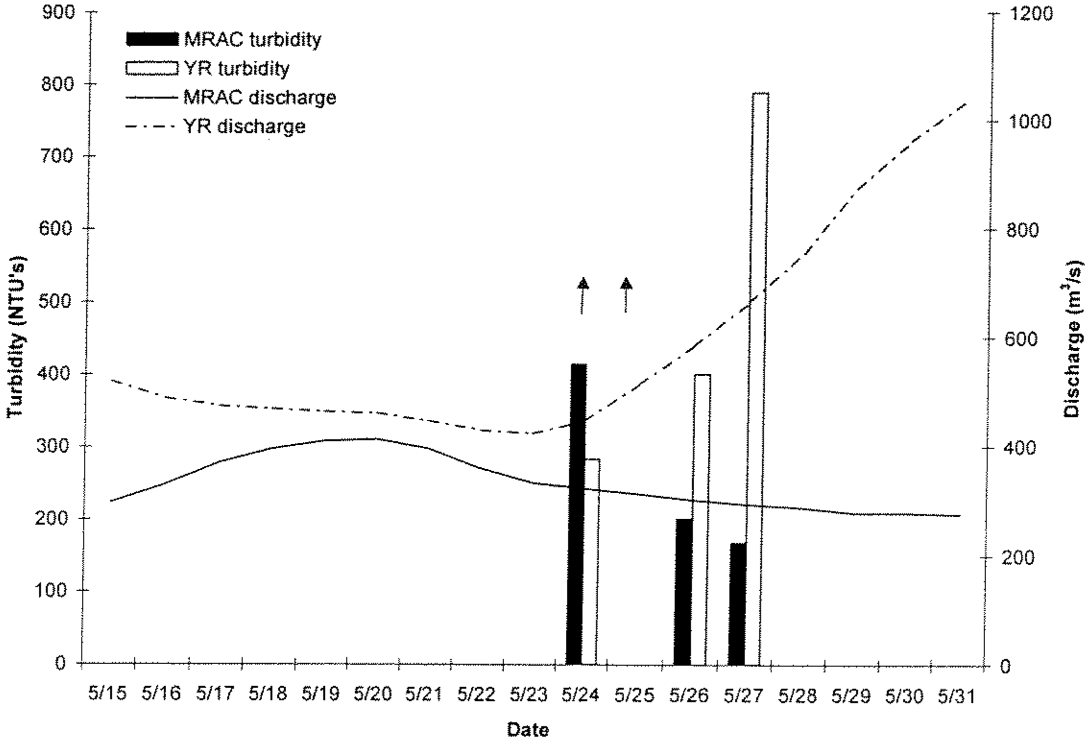


Figure 11. Comparison of river discharge and turbidity in the YR and MRAC during the time period in which radio-tagged paddlefish were contacted in the MRAC in 2000. Arrows indicate when fish were contacted in the MRAC after a previous contact either in the MRBC or the YR. Though not depicted in the graph, one fish was contacted in the MRAC on June 3 after a previous contact in the MRBC on April 25.

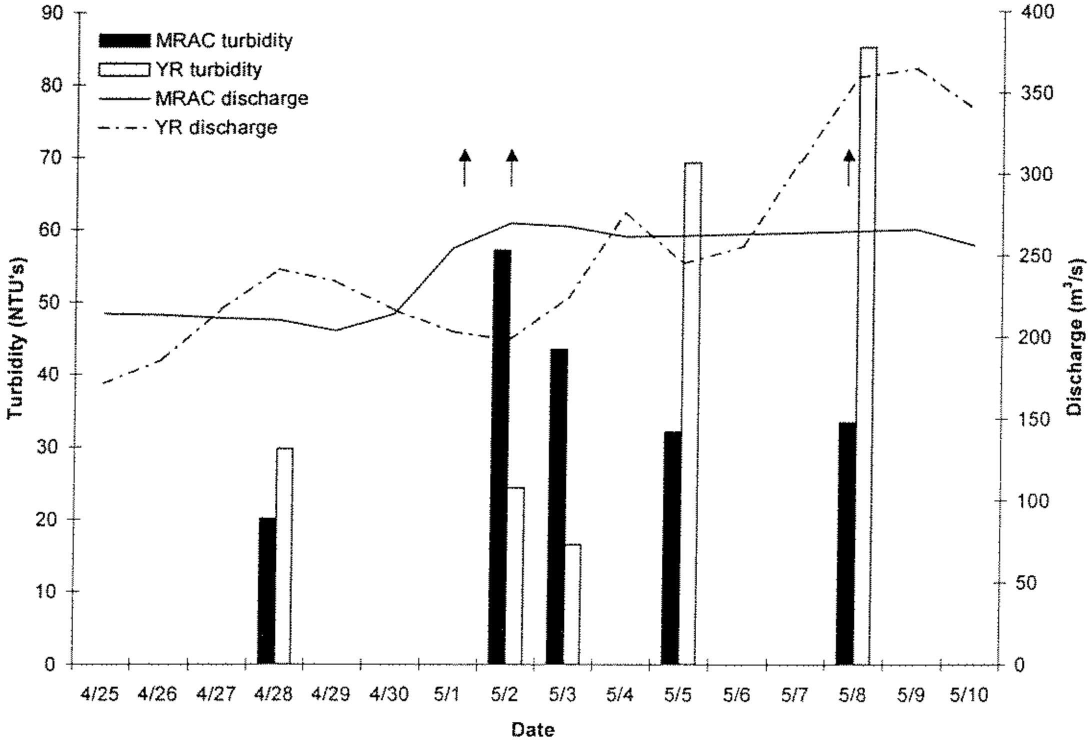


Figure 12. Comparison of river discharge and turbidity in the YR and MRAC during the time period in which radio-tagged paddlefish were contacted in the MRAC in 2001. Arrows indicate when fish were contacted in the MRAC after a previous contact either in the MRBC or the YR. Arrows at May 18 and 25 belong to one fish that was contacted at the Confluence during the intervening time period.

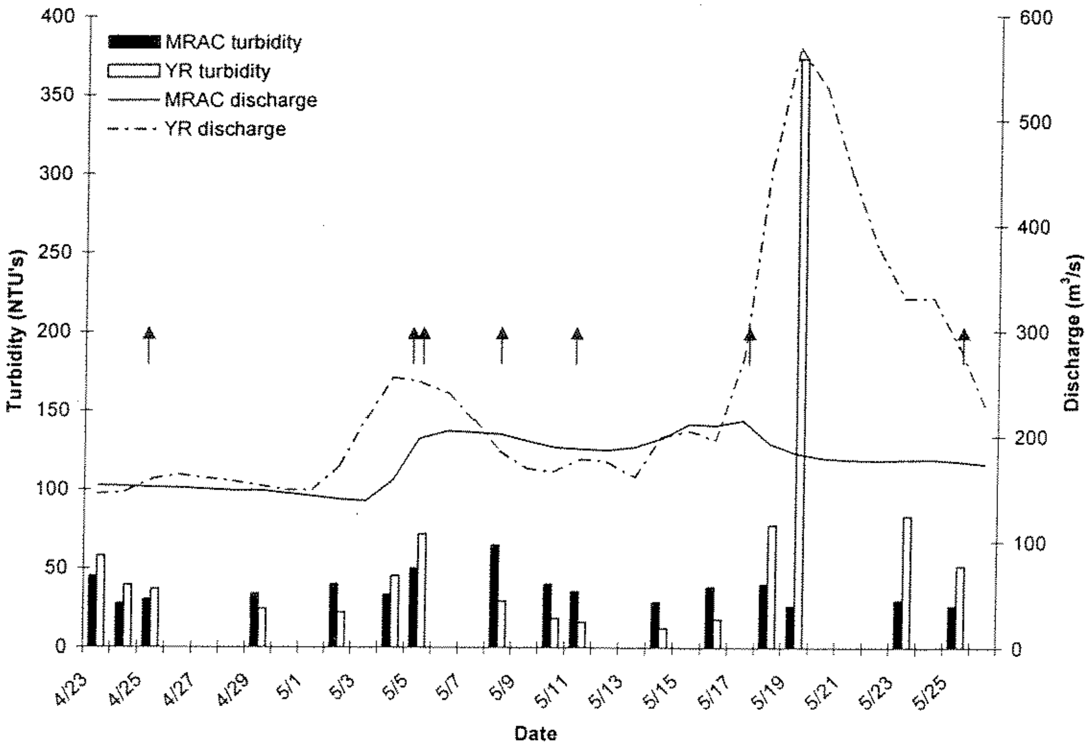


Figure 13. Comparison of river discharge and turbidity in the YR and MRAC during the time period in which radio-tagged paddlefish were contacted in the MRAC in 2002. Arrows indicate when fish were contacted in the MRAC after a previous contact either in the MRBC or the YR. The number in parentheses indicates the number of fish that were contacted in the MRAC during the survey date.

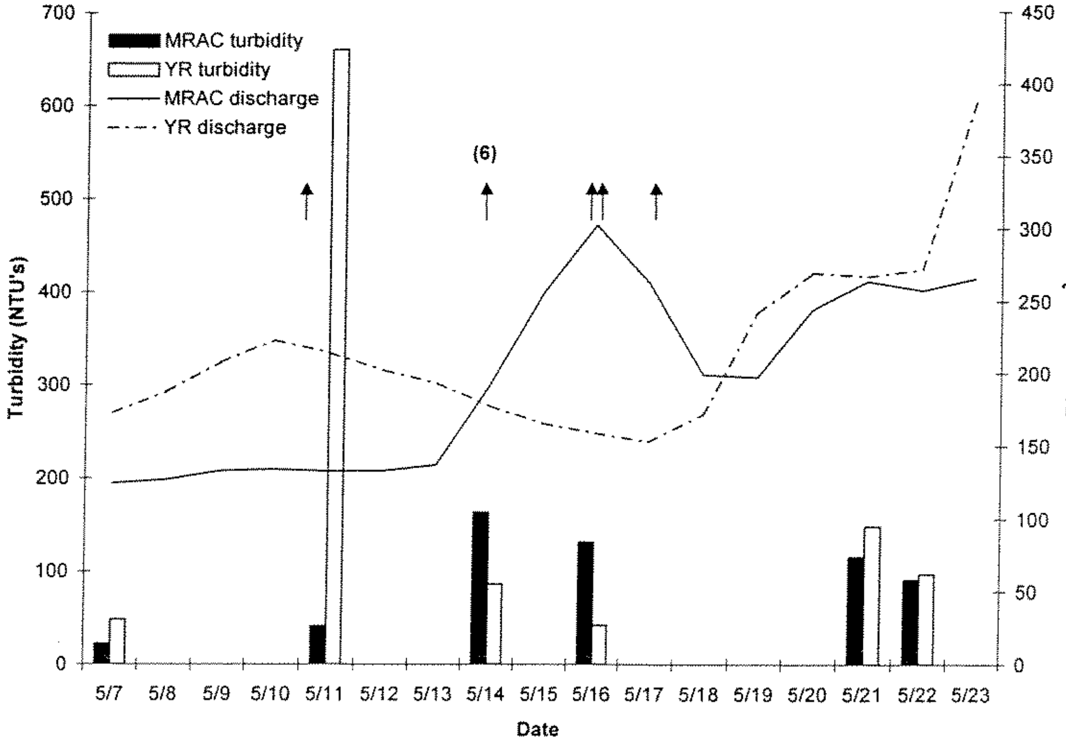


Figure 14. Model predictions of river selection for radio-tagged paddlefish that ascended the YR (n=15) and the MRAC (n=11) during short time periods in the spring migrations of 2000-2002. Probabilities greater than 0.5 indicated that paddlefish were predicted to ascend the YR, whereas probabilities less than 0.5 indicated that paddlefish were predicted to ascend the MRAC. The small, medium, and large open circles represent periods of YR ascension for one, two, and three fish, respectively. The small and large crosses represent periods of MRAC ascension for one and two fish, respectively.

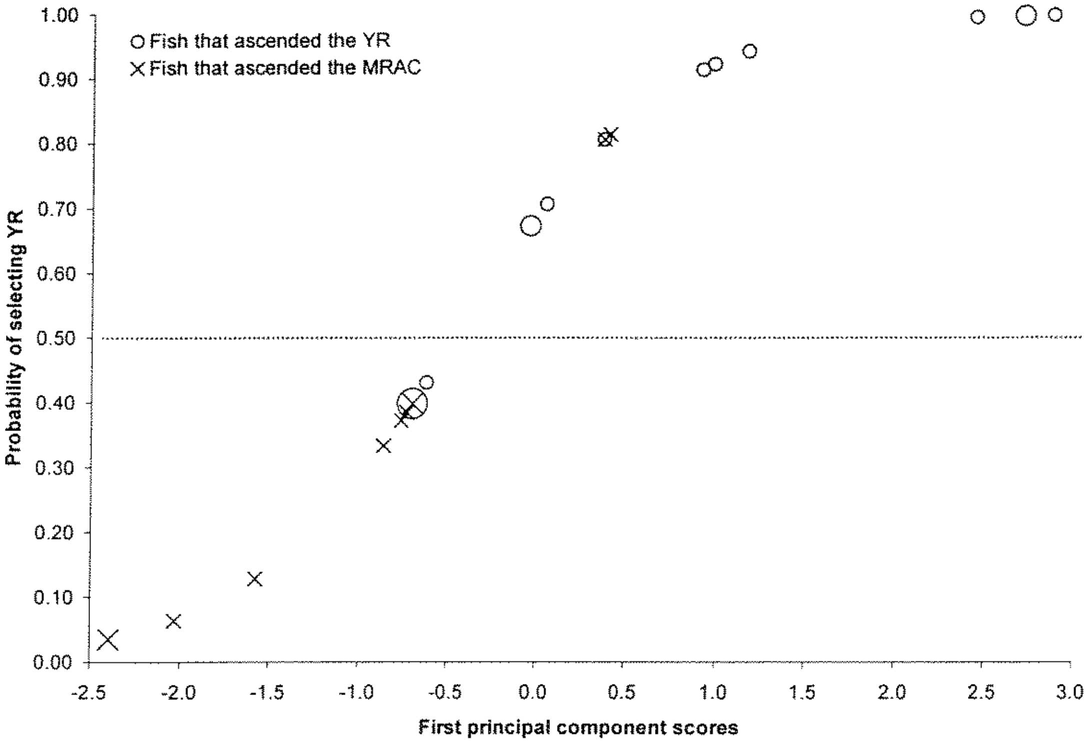


Figure 15. Distribution of furthest river kilometers attained by radio-tagged paddlefish during the spring migrations of 1999-2002. Numbers in parentheses indicate the number of females (F), males (M), and fish of unknown sex (U) for each year. Positive and negative values indicate the number of kilometers up the YR and below the Confluence, respectively; dashed horizontal line represents the Confluence.

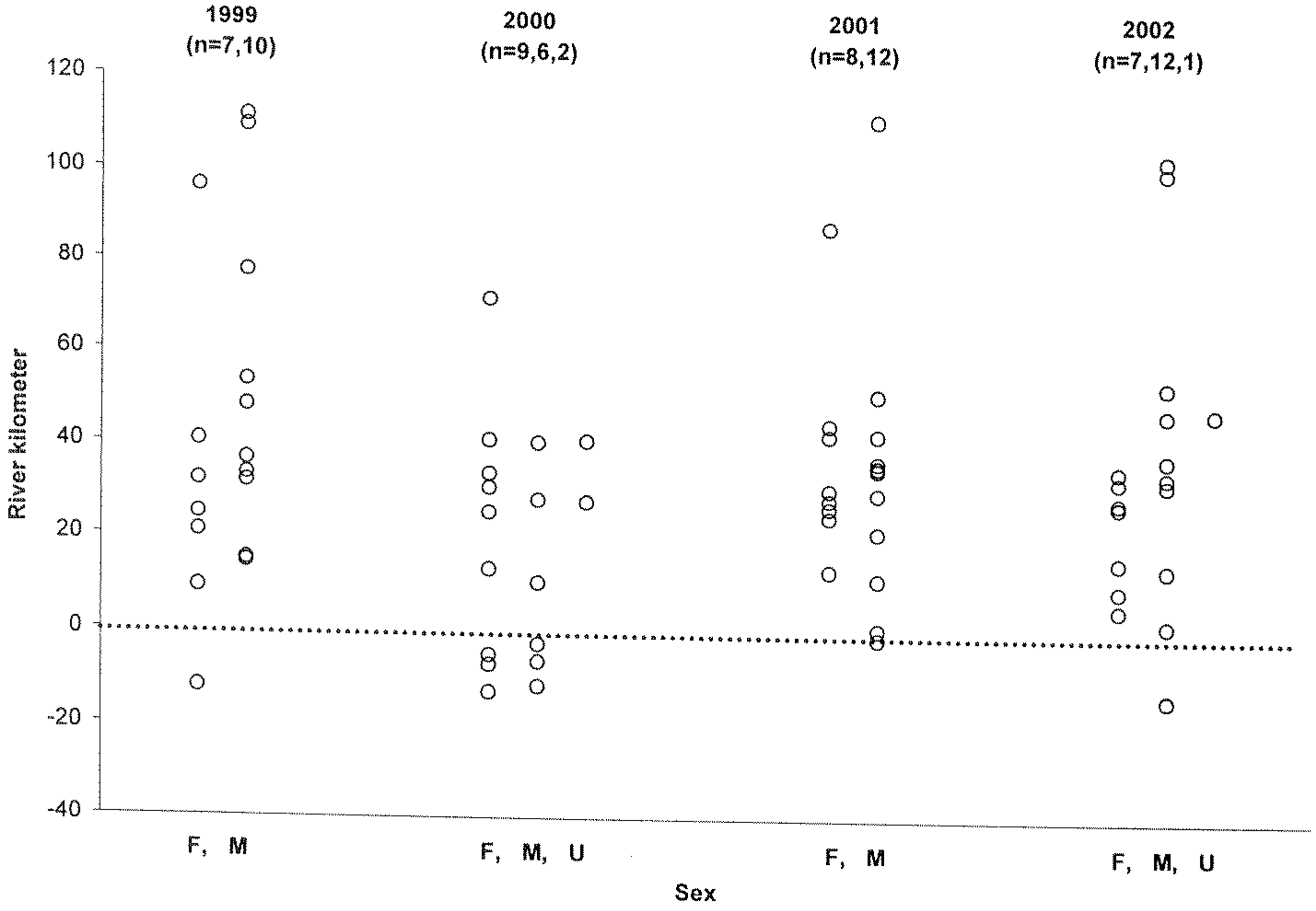


Figure 16. Distribution of river kilometers where radio-tagged paddlefish were last contacted during spring migrations of 1999-2002. Positive and negative values indicate the number of kilometers above and below the Confluence, respectively; dashed horizontal line represents the Confluence.

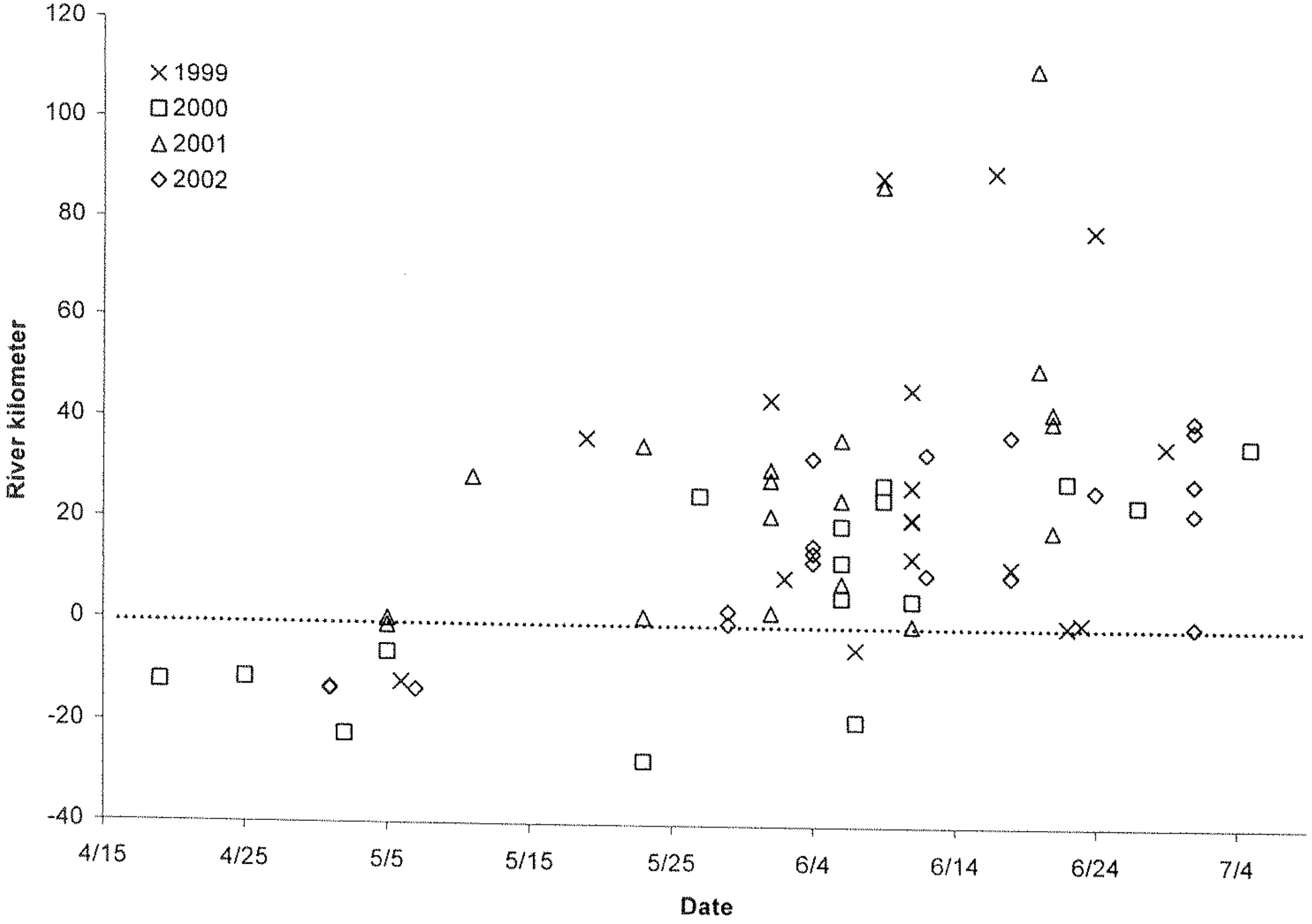


Figure 17. The percentage of radio-tagged paddlefish that were still contacted in the river system as spring advanced during the migrations of 1999-2002. Symbols plotted along each line represent dates when at least one of the tagged fish was last contacted along the river system. The two vertical dotted lines bracket the time period in which many of the paddlefish were last contacted in each of the four years.

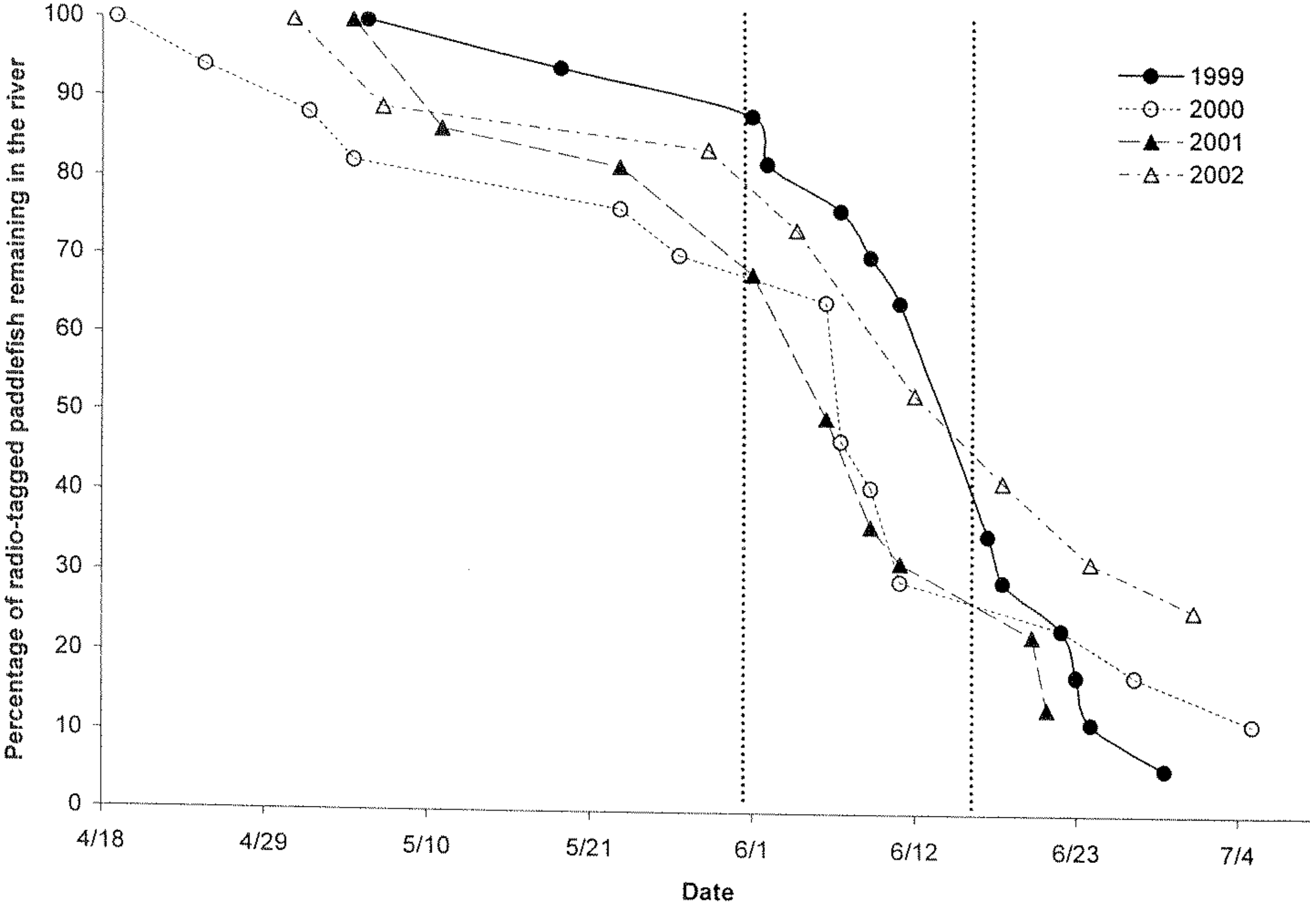


Figure 18. The distribution of radio-tagged paddlefish contacts along the MR during the falls of 1999-2001. Reaches indicate the number of river kilometers below the Confluence.

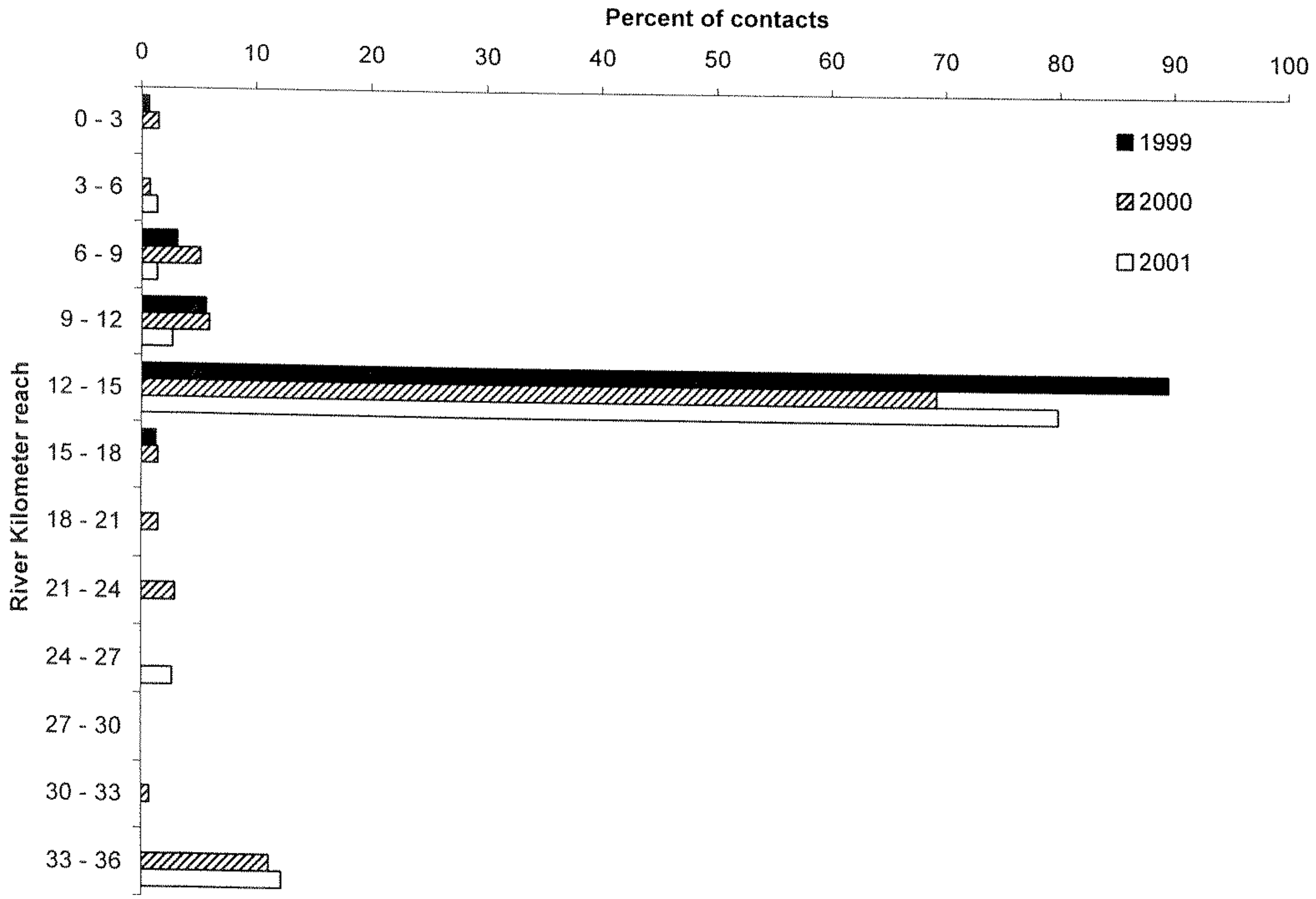
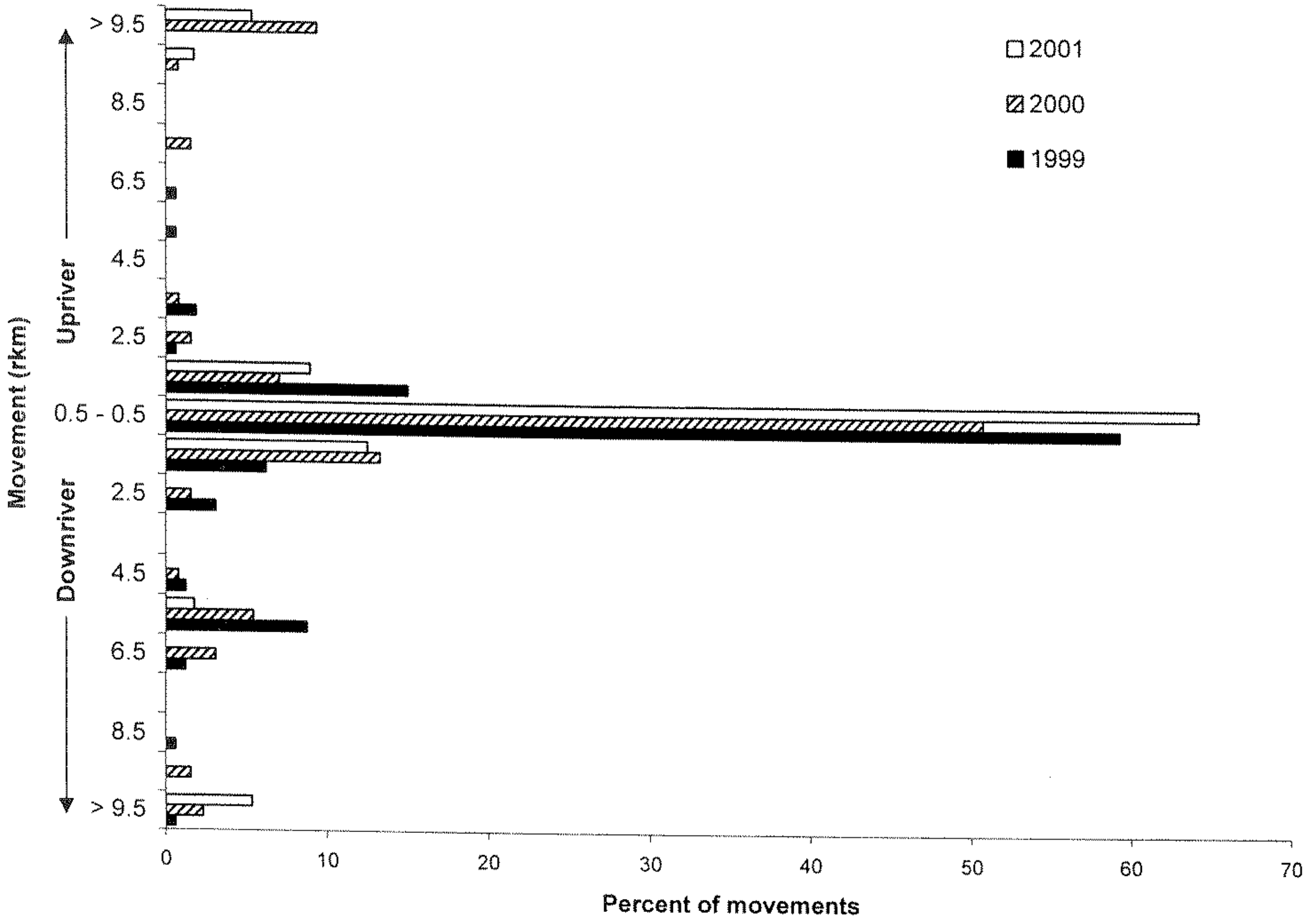


Figure 19. The distribution of radio-tagged paddlefish directional movements along reaches of the MRBC during the falls of 1999-2001. Movements are separated into 1 rkm bins (e.g. 2.5 indicates movements between 1.5 and 2.5 rkm).



CHAPTER 2. The detection of paddlefish spawning activity along the lower Yellowstone River through the collection of eggs along a suspected incubation reach

ABSTRACT

A passive egg sampling technique was developed in order to confirm egg incubation sites and describe the temporal variability in spawning for paddlefish, *Polyodon spathula*, along the lower Yellowstone River. Egg collectors modeled after the mats used in sturgeon research were difficult to retrieve and did not collect eggs during the 2000 sampling season. Tubular egg collectors proved to be more practical and were successfully retrieved 97% of the time during 2001 and 2002. One hundred and thirty Acipenseriform eggs were collected along the suspected incubation reach and 99% of the identifiable eggs were genetically confirmed as paddlefish. During both years, egg catch-per-unit-effort (CPUE) peaked in mid-June after peak periods of Yellowstone River discharge. River temperatures were typically increasing and between 15-22°C during periods in which eggs were collected. Average egg CPUE was lower during the low flow year of 2001 (0.11 egg/collector/d) than during 2002 (0.39 egg/collector/d). During peak collection periods in 2001 and 2002, 20 and 45% of the collectors had at least one egg, respectively; 83% of the eggs were found on collectors retrieved from the channel thalweg. However, mean egg counts were low (< 4 eggs/collector) suggesting either low collector efficiency, the inability to place collectors near the vicinity of concentrations of spawning paddlefish, or the distribution of spawning effort over a large portion of the lower Yellowstone River.

INTRODUCTION

Paddlefish, *Polyodon spathula*, occupy large river habitats within the Mississippi River system and selected Gulf slope drainages. Although found within twenty-two states of the central and southeastern United States, their range and abundance have diminished from historic distributions, even in areas once considered strongholds (Hoxmeier and DeVries 1996; Graham 1997). The declines have been mainly attributed to large river modifications that have not only eliminated productive rearing habitats but created conditions less favorable for successful reproduction (Sparrowe 1986). Impoundments have impeded adult spawning migrations and inundated suitable spawning habitat. In addition, the alteration of river temperature and the natural hydrograph by dams has disrupted the stimuli used by paddlefish during the spring spawning migration (Unkenholz 1986; Hesse and Mestl 1993).

Although general requirements for successful reproduction of paddlefish in the wild have been described, many details remain unknown. Paddlefish have been found to broadcast their eggs over well-swept gravel bars coincident with periods of rising temperature and discharge during the spring (Purkett 1961; Pasch et al. 1980; Russell 1986). Gravel-rubble substrate provides suitable attachment sites for the adhesive eggs, whereas adequate current velocity prevents siltation during the incubation period (6-12 days depending on temperature; Yeager and Wallace 1982). Spawning habitats have typically been identified along tailwater reaches where paddlefish tend to concentrate during the spawning migration (Pasch et al. 1980; Wallus 1986; Lein and DeVries 1998). However, spawning and egg incubation reaches have not been delineated for most stocks (Jennings and Zigler 2000). Because of the poor natural recruitment of many stocks and the potential for unidentified spawning habitat to be altered through ongoing modifications of large-river habitats, it is important to better understand paddlefish spawning habitat.

Sexually mature, migratory paddlefish of the Yellowstone-Sakakawea stock of eastern Montana and western North Dakota are found along the lower Yellowstone River during the spring spawning period (Robinson 1966; Rehwinkel 1978). Although larval collections have demonstrated paddlefish reproduction in the lower river reaches (Gardner 1996; Liebelt 1996), egg incubation sites have not yet been identified. It is not known whether sites are confined to specific reaches, or if they are widely scattered. In order to preserve existing spawning habitat, it is necessary to determine the distribution of these sites along the lower Yellowstone River.

Various techniques have been used to identify paddlefish spawning habitat. Purkett (1961) first identified egg incubation sites through direct observation along the Osage River, Missouri. After a brief rise in discharge, receding water levels revealed exposed eggs along gravel bars. Active methods such as plankton nets or epibenthic sleds have also been used to identify spawning events along various river systems (Pasch et al. 1980; Wallus 1986; Hesse and Mestl 1993). However, these methods have been more successful in sampling larvae than eggs. In addition, spawning and egg incubation sites can not be identified accurately based on the capture of larval fish because of variable larval drift rates.

Artificial substrate mats have proven to be an effective technique for the identification of spawning sites for various sturgeon populations (Marchant and Shutters 1996; Fox et al. 2000; Paragamian et al. 2001; Perrin et al. 2003). As with paddlefish eggs, the highly adhesive sturgeon eggs sink after they are broadcast by spawning adults. As a result, eggs collected by mats positioned along the river bottom are assumed to have been spawned in the vicinity. Mats may be more likely to detect spawning events than active sampling methods because they can be deployed continuously for periods as long as several days. In addition, mats may be less likely to get entangled along bottom obstructions, and can be deployed in areas where high current velocities may prevent the use of other sampling techniques. Although mats have proven effective in locations where substrate is relatively stable, it was unknown if they would be effective in the lower Yellowstone River which is characterized by unstable, shifting substrate.

A pilot egg collection study was conducted along the lower Yellowstone River during paddlefish spawning periods of 2000 through 2002. The primary objective was to determine if artificial substrate collectors could be used as a sampling method to collect eggs and confirm suspected incubation reaches along the lower river. The temporal patterns of collected eggs were also characterized in an attempt to relate spawning to seasonal environmental cues along the Yellowstone River.

STUDY SITE

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. Adults that are reproductively ripe move out of the reservoir and migrate upriver to spawn during the spring. Many of the paddlefish ascend into the lowermost 110 km of the Yellowstone River, a quasi-natural stretch which extends upriver from its confluence with the Missouri River (hereinafter referred to as the

Confluence) to the Intake Diversion Dam near Glendive, Montana (Figure 1). The 70 km reach of the river below Intake contains multiple islands and alluvial channel bars with substrate consisting primarily of cobble and gravel. Although in-channel features remain common along the lowermost 40 km of the river, sand replaces gravel as the predominant substrate (Bramblett 1996). Because the Yellowstone River remains undammed, it has retained a natural hydrograph with high levels of discharge and sediment load during the spring. Some adult paddlefish also ascend the regulated Missouri River up to 300 river kilometers (rkm) from the Confluence to the tailwaters of Fort Peck Dam (Figure 1). In contrast to the lower Yellowstone River, the Missouri River between Fort Peck Dam and the Confluence has lower discharge, less sediment load, and lower river temperatures during spring (Gardner and Stewart 1987; Hesse 1987).

METHODS

Field techniques

Sampling was conducted only along the lower Yellowstone River because previous tagging studies have indicated that spawning paddlefish primarily used the Yellowstone River, rather than the Missouri River (Robinson 1966; Rehwinkel 1978). Because of the exploratory nature of the study, sample sites were not distributed over the entire length of the lower Yellowstone River but chosen to maximize the likelihood of collecting eggs. Previous research by Gardner (1993, 1995, 1996) revealed potential incubations sites along the lower 32 rkm based on the collection of larval paddlefish along specific reaches during consecutive sampling seasons. Logistical constraints permitted only four potential incubation sites to be sampled along this lower stretch: rkm

9.5, rkm 13.5, rkm 21.5, and rkm 25.5 (hereinafter designated as sites 1, 2, 3, and 4 respectively; Figure 2). A general description of the physical characteristics of all four sites is provided in Table 1. Although substrate consisted primarily of sand along most of the lower 32 rkm, substrate samples indicated that gravel was present at all of the sites, and tactile sampling using a long-handled wooden probe indicated that boulders or bedrock was present at the three upriver sites (Figure 2). In addition, concentrations of paddlefish had been observed in the vicinity of all four sites during an on-going radio-telemetry study supporting the potential of these sites as spawning reaches.

The first type of egg collectors used were mats of artificial substrate designed and used successfully by McCabe and Beckman (1990) for collecting white sturgeon, *Acipenser transmontanus*, eggs in the Columbia River. Furnace-filter material, which provided a rough surface for egg attachment, was fitted and secured between complementary 0.60 by 0.75 m angle-iron frames. Each mat was equipped with a 4.5-5.0 kg rebar grapple anchor and a buoyed 12.0-15.0 m hauling line. Mats were deployed from May 25 through June 16, 2000. The use of the mat design was permanently discontinued after June 16 because some of the mats became covered by shifting substrate and could not be retrieved.

A different type of collector, tubular in design, was constructed in 2001. Two strips of furnace-filter material (0.75 m wide) were fitted and secured around a PVC cylinder 1.5 m in length and 0.15 m in diameter. Two 4.5-5.0 kg anchors were secured to the tube, one at each end, and a buoyed hauling line was attached to the middle. Because the open-ended tube was more likely to be suspended off the bottom than the iron frame, the intent of this design was to reduce the possibility that shifting substrate would bury the tubes. However, this long tube design was also discontinued after initial deployment on May 18 due to retrieval difficulties.

A third type of egg collector, a short tube, was then constructed later in 2001 to both reduce collector size and minimize prolonged contact with the river bottom (Figure 3). A single strip of furnace filter material (0.75 m wide) was fitted and secured around a PVC cylinder 0.75 m in length and 0.15 m in diameter. A single 4.5-5.0 kg anchor was then attached to one end and a buoyed hauling line to the other end of the tube. This short tube design was used from May 28 to June 22, 2001, and from May 24 to June 27, 2002.

During the spring of 2000, sites 2, 3, and 4 were sampled. During 2001, only site 2 was sampled in order to determine the usefulness of the newly-designed tubes. During 2002, sites 1 and 2 were sampled. Dates of first deployment were determined using a combination of the following information: (1) approximate dates when paddlefish larvae were first collected during previous years, (2) the rise of water temperatures above 10°C, the lower spawning threshold reported for paddlefish (Crance 1987; Jennings and Zigler 2000), and (3) the appearance of ovulated eggs from harvested adult paddlefish in the Missouri and Yellowstone Rivers. Sampling was discontinued when tagged fish from an on-going telemetry study were no longer contacted in the river (indicating descent into the reservoir and probable cessation of spawning activity), and when water temperatures exceeded 23°C, the upper thermal limit reported for spawning paddlefish (Hoxmeier and DeVries 1997).

Three to five egg collectors were deployed equidistantly as a set across the river channel at each site. The number of sets deployed ranged between one and three depending on the apparent size of the potential incubation area. Depth and channel position were recorded for each deployed collector. Every 2 to 5 d, collectors were retrieved and examined for the presence of eggs. Acipenseriform eggs, identified by color and size, were removed and preserved in 80% ethanol. Collectors were then rinsed thoroughly before being deployed back into the river. Although eggs were not analyzed to determine their developmental stage, outward indications of embryonic development were noted. Because sturgeon (*Scaphirhynchus sp.*) were also present in the study area, eggs were sent to the National Fish and Wildlife Forensics Laboratory in Ashland, Oregon for species identification. Mitochondrial DNA sequences from a region of the cytochrome *b* gene were obtained from the eggs and compared to reference sequences from paddlefish, pallid sturgeon, *Scaphirhynchus albus*, and shovelnose sturgeon, *S. platorhynchus*. The genetic methods and analyses used are described in Straughan et al. (2002).

Data Analyses

Sampling effort expended at each site, or collector days, was calculated as the number of retrieved collectors multiplied by the duration of the set. Catch-per-unit-effort (CPUE; eggs/collector/d) was calculated as an index of egg abundance at each site, and was used to draw comparisons among years, and to relate spawning events to changes in Yellowstone River conditions. Daily Yellowstone River discharge (m^3/s) and suspended sediment (mg/L) data were obtained from the United States Geological Survey (USGS) gauging station near Sidney, Montana (rkm 47), and river temperatures were obtained from a temperature logger positioned at Yellowstone rkm 13.5.

Likelihood models were constructed to assess differences in the spatial distribution of collected eggs among sites. Models were only developed for 2002 egg count data because eggs were not collected in 2000 and only a small number of eggs were collected in 2001. In addition, models only included those eggs collected along the thalweg during the four sample periods from June 8 to 25 (denoted as periods a, b, c, d). Because eggs were likely to be highly clumped if they were released near the collectors, a negative binomial distribution, which relaxes the assumption of spatial independence and allows for overdispersed data, was used to model the egg counts (Bliss and Fisher 1953; White and Bennetts 1996). The parameters of the negative binomial model included a mean egg count, m, and a dispersion factor, k, which described the degree of clumping: as $k \rightarrow 0$, eggs were highly clumped, whereas as $k \rightarrow \infty$, eggs were randomly (i.e. Poisson) distributed. Differences in the parameters between sites were assessed by judging the relative likelihood of restricted models (models 2-4, 6-8, and 10-12) to fully parameterized models (models 1, 5, and 9; Table 4). Candidate models included those where mean counts were allowed to vary by sample period (models 1-8). In order to reduce the number of estimated parameters, a subset of models also included those which described a temporal relationship among mean counts: mean counts, initially estimated as m, were modeled to decrease linearly to 0 after a certain sample period (models 5-8). The information-theoretic approach was used to evaluate the relative plausibility of the candidate probability models (Burnham and Anderson 1998). Akaike's Information Criteria (AIC), corrected for a small sample size, was used to determine the best approximating model. AIC differences between the best model and other candidate models (Δ_i) were calculated and used to judge the relative likelihood of each model: a difference less than 2 indicated that the model had substantial support as the best model (Burnham and Anderson 1998).

RESULTS

During the study period, 338 collectors were deployed for a total of 1193 collector days (Table 2). Less effort was expended in 2000 than in 2001 and 2002 due to the foreshortened sample period and the number of mats lost. During 2000, 56 of the 71 (79%) mats were recovered during initial retrieval attempts. Three mats were later recovered after elapsed periods of 29 to 37 d. Mats were most likely temporarily buried by shifting substrate as it was difficult to dislodge them from the riverbed. Similarly, only 3 of the 12 (25%) long tubes were retrieved after their deployment on May 18, 2001. The long tubes were also difficult to retrieve and were evidently filled with bed load material.

Ninety-seven percent of the short tubes were retrieved successfully during both 2001 (88 of 91) and 2002 (159 of 164) (Table 2). Although the tubes typically were retrieved from the location where they had been deployed, debris accumulated along hauling lines during periods of rising discharge and tubes were often recovered downriver from the point of deployment. As a result, the tubes were temporarily removed from the river for a period of 2 d in 2001 (June 17-18) and 5 d in 2002 (June 3-7) because of large amounts of debris transported down the river at these times.

Although eggs were not found at any of the sample sites during 2000, 130 Acipenseriform eggs were collected during 2001 and 2002. Most of the eggs were collected after the first week in June during both years (Table 3). Seventeen eggs were collected in 2001 and were found on 20% of the tubes retrieved from June 8 to 22. One hundred and five eggs were collected during 2002 and all but one were found on 45% of the tubes retrieved at each site from June 8 to 25. Eight additional eggs were found on a mat recovered at site 2 during 2002 from a 2000 deployment. Although eggs were not analyzed to determine the percentage of developing embryos, tail buds were apparent on several of the collected eggs during both years. Eighty-nine of the ninety identifiable eggs (99%) were genetically confirmed as paddlefish eggs; one egg was determined to be a sturgeon species, either shovelnose sturgeon or pallid sturgeon. Poor sample quality likely contributed to the inability to genetically differentiate the other forty eggs.

Peak egg CPUE was often associated with the declining limb of the Yellowstone River hydrograph (Figure 4). During 2001, peaks in egg CPUE occurred during sample periods June 8-12 (0.12 eggs/collector/d) and June 19-22 (0.21 eggs/collector/d) after river discharge and turbidity peaked on June 6 and 17, respectively. Average daily river temperature during the two collection periods ranged from 18 to 22°C. During 2002, egg CPUE peaked during sample period June 13-17 at both sites 1 and 2 (0.46 and 0.65 eggs/collector/d, respectively) after discharge and turbidity peaked on June 6 (Figure 4). One egg was also collected after a smaller rise in discharge that peaked on May 25. Average daily river temperatures ranged from 15 to 22°C during the periods in which eggs were collected in 2002.

Egg collection rates at site 2 were lower in 2001 than in 2002 (Table 3; Figure 4). The average of the three highest CPUEs was 0.11 eggs/collector/d in 2001 and 0.39 eggs/collector/d in 2002. Similarly, average discharge during June was lower in 2001, 422 m^3/s, than in 2002, 670 m^3/s (Figure 4). In addition, Yellowstone River discharge fluctuated considerably during the spring of 2001 with periods of continuously increasing flow lasting no longer than 5 d.

Eggs were found at depths between 1.2 and 4.9 m. However, the depths at which eggs were found differed between the two sites in 2002 (Figure 5). Although tubes at site 1 were deployed across the channel at depths between 2.0 and 5.0 m, 90% of the tubes with eggs were located at depths greater than 3.5 m. At site 2, the depthwise distribution of deployed tubes and tubes with eggs was similar with approximately 90% located at depths between 1.5 and 3.0 m. The between-site difference in the range of depths at which eggs were collected was predominantly due to the deep thalweg along the west bank at site 1.

Eggs were typically found on tubes retrieved from the channel thalweg at both sites. In 2001, seven of the nine tubes with eggs were retrieved from the mid-channel thalweg at site 2 and these seven tubes accounted for 65% of the eggs collected that year. In 2002, 17 of the 26 (65%) tubes with eggs were retrieved from the middle of the channel and these 17 accounted for 82% of the eggs collected at site 2 that year (Figure 6). At site 1, 9 of the 11 (82%) tubes with eggs were retrieved along the thalweg near the west bank and accounted for 94% of the eggs collected at that site in 2002 (Figure 6).

Eggs collected at both sites were most often found in low numbers on a given tube. In 2001, only one or two eggs were found on all but one of the nine tubes that had collected eggs at site 2 (Table 3). In 2002, fewer than four eggs were found on 27 of the 36 (75%) tubes that had collected eggs at both sites during the peak collection period (Figure 6). Estimated mean counts did not exceed 4 eggs/collector for all three of the models (models 4, 7, 8) that were considered to have support as the best model describing the distribution of eggs collected along the thalweg at both sites (Table 4). In addition, model results indicated that the estimated means of the egg distributions were not different between the two sites. However, site-specific dispersion parameters were estimated for one of the models (model 7) receiving support as the best approximating model. The lower estimated dispersion parameter at site 2 (0.63) than at site 1 (1.76) suggested a more clumped distribution of eggs at the upriver site. Nine or more eggs were found on three collectors at site 2 whereas the greatest number of eggs found on a collector at site 1 was six (Figure 6).

DISCUSSION

The short tubes used during 2001 and 2002 proved to be a viable passive technique for collecting paddlefish eggs in a river system with unstable, shifting substrates. The tubes were successfully retrieved over 95% of the time and collected eggs during both years. In comparison, the egg mats used during 2000 often became buried in substrate and were difficult to dislodge from the riverbed. Paragamian et al. (2001) also found egg mats to become buried by shifting substrates during high flow events in their efforts to document white sturgeon (*Acipenser transmontanus*) spawning events in the Kootenai River, Idaho. Although mats that are temporarily buried may later be recovered, the sample design is still compromised. The permanent loss of mats is also more costly than the loss of tubes because of the more expensive materials used in their construction.

Genetic analyses revealed that over two-thirds of the eggs identified as probable Acipenserids were paddlefish eggs. However, the eggs that could not be identified were often found on the same tube as confirmed paddlefish eggs thus increasing the likelihood that the unknown eggs were also paddlefish eggs. It is unknown if the egg identified as *Scaphirhynchus* was a shovelnose sturgeon or pallid sturgeon since sympatric populations exist along the lower Yellowstone River. Even though Bramblett and White (2001) found that during the spawning season radio-tagged pallid sturgeon were contacted more often than shovelnose sturgeon along the reach in which the egg was collected, shovelnose sturgeon are much more abundant than pallid sturgeon in the lower Yellowstone River. Therefore, the egg was more likely to be from a shovelnose sturgeon.

The collection of paddlefish eggs at rkm 9.5 and 13.5, along with the observation of developing embryos, supports the existence of paddlefish incubation sites within this stretch of the lower Yellowstone River. This is consistent with previous larval collections as paddlefish have been regularly collected along the lower 30 rkm with high densities found along rkm 13.5 (Gardner 1993, 1995, 1996). On the other hand, the high percentage of eggs collected along the thalweg at both sites may be indicative of only egg interception and not egg deposition along the lower Yellowstone River. Assuming that collectors at both sites were equally likely to intercept eggs drifting along the bottom of the four km reach, the narrow, constricted channel thalweg along the downriver site would tend to concentrate drifting eggs and give rise to higher egg densities on collectors along the downriver site than along the upriver site. However, our results indicated a similar mean collection rate between sites and a higher degree of clumping at the upriver site than at the downriver site. Furthermore, eight eggs were found on a retrieved egg mat, which presumably lay flush with the river bed, at the upriver site. This suggests egg deposition along rkm 13.5 and the occurrence of residual drift from that site down to rkm 9.5. The availability of large substrate (i.e. gravel and bedrock) at rkm 13.5 would provide firm attachment sites for the adhesion of eggs. The availability of other physical characteristics at rkm 13.5 that would facilitate egg deposition and adhesion, such as the presence of eddy currents, needs further investigation (Sulak and Clugston 1998; Perrin et al. 2003). Although eggs were not collected at rkm 21.5 and 25.5, two other sites identified by Gardner as probable incubation reaches, the ineffectiveness of the mats and the discontinuation of sampling by mid-June of 2000 may have prevented the detection of spawning activity along these reaches.

The clumped distribution of eggs along Yellowstone rkm 13.5 may also indicate that eggs were released by spawning females within the vicinity. However, the overall low mean number of eggs found on collectors suggests either a low collector efficiency (i.e. collecting a small percentage of the available eggs) or an inability to deploy collectors in close proximity to concentrations of spawning paddlefish. Though published accounts of passive egg collection techniques for paddlefish are scarce, comparisons may be drawn to similar studies in which sturgeon spawning sites had been identified. Paragamian et at. (2001) collected 349 white sturgeon eggs on 44 mats (average of 8 eggs/mat) during the 1996 sampling season on the Kootenai River. Groups of up to 63 gulf sturgeon (*Acipenser oxyrinchus desotoi*) eggs were found on individual samplers deployed along the Suwanee River, Florida (Sulak and Clugston 1998). McCabe and Beckman (1990) recorded counts up to 423 white sturgeon eggs on individual mats set below Bonneville Dam on the Columbia River. During lake sturgeon egg sampling efforts on the Wolf River, Kempinger (1988) calculated seasonal means of

1,035 to 8,805 on 1-m^2 trays set along spawning areas. In all these cases where collection rates were higher than in our study, fish were either highly concentrated in certain reaches (e.g. below dams) during the spawning season, or efforts were focused along suspect spawning areas previously identified through telemetry, visual observation, or other sampling techniques. Conversely, Perrin et al. (2003) collected only 77 white sturgeon eggs on 221 deployed mats along the unregulated Fraser River and concluded that this was due to the widespread distribution of both spawners and spawning habitat. Similarly, only 42 gulf sturgeon eggs were collected at widely-distributed sites along the Choctawhatchee River system where previous knowledge of specific sturgeon spawning areas was unavailable (Fox et al. 2000). In general, when spawning sites were precisely known or the fish were visible, egg collection efficiency increased.

In our study, the low number of paddlefish eggs collected may be due to the widespread distribution of spawners as well as a lack of information concerning specific paddlefish spawning sites. Telemetry data (unpublished) have indicated that fish are not concentrated within a few reaches during the spawning season, and that upriver movements do not cease at specific sites but are extensive and bi-directional throughout the spawning migration. The distribution of spawning effort over a large expanse of the lower Yellowstone River may benefit paddlefish by reducing the risk associated with such a spatially unpredictable reproductive environment (den Boer 1968). The low sampling effort relative to the size of the potential spawning area also likely contributed to our inability to place collectors near groups of spawning paddlefish. On the other hand, the low egg counts may be representative of typical deposited egg densities along incubations sites. It is not known where in the water column paddlefish spawn and the current may likely disperse the released eggs widely as they drift downriver before adhering onto substrate (Purkett 1961).

The importance of discharge as a stimulus that triggers spawning in paddlefish was indicated by the collection of eggs after peak periods of Yellowstone River flow during the study period. These results are consistent with previous work by Gardner (1993, 1995, 1996) along the lower Yellowstone River in which larval paddlefish were typically collected 10 d after peak discharge (assuming a 6-7 d hatching period; (Yeagar and Wallace 1982)). Indicators of spawning activity have been associated with discharge and specifically the declining limb of the hydrograph in other paddlefish stocks as well (Purkett 1961; Wallus 1986; Lein and DeVries 1998). Similar results have also been found for other large river migratory fishes such as white sturgeon (Perrin et al. 2003), shortnose sturgeon, *Acipenser brevirostrum* (Kieffer and Kynard 1996), and Colorado pikeminnow, *Ptychocheilus lucius* (Haynes et al. 1984; Tyus 1990). The synchronization of spawning with external cues that signal a favorable incubation environment would benefit fishes that reproduce in such unpredictable large-river environments (Cohen 1967; Giesel 1976; Stacey 1984). Spawning during the declining limb of the hydrograph may increase the chance for egg adhesion onto substrates and decrease the likelihood that heavy currents will scour deposited eggs or flush emerging larvae into unfavorable areas. Shallow, slow current velocity areas also increase during the recessional period of the hydrograph which may provide favorable habitat for the growth and survival of newly-emerging larval fish (Bowen et al. 2003).

However, the near absence of eggs on collectors during peak periods of Yellowstone River discharge in May of both years suggests that, though discharge may be the triggering stimulus, a combination of other environmental cues was required before paddlefish were ready to spawn. Although temperature has been considered an important factor in controlling the timing of spawning in paddlefish (Russell 1986; Wallus 1986; Pasch et al. 1980), temperatures considered adequate for spawning (i.e. above 14°C) were present along the Yellowstone River during May of both years. It is likely that photoperiod interacts with temperature to control the timing of spawning in paddlefish as has been found in other species of fish (Bye 1984). In addition, the number of degree days above a thermal threshold may be equally influential as the rate of warming in regulating the final stages of gamete maturation during late winter and early spring. The long, cold winters in northerly latitudes may thus explain the detection of spawning along the Yellowstone River at dates later than those reported for paddlefish along more southerly river systems (Pasch et al. 1980; Wallus 1986; Hoxmeier and DeVries 1997; Lein and DeVries 1998).

The lower egg collection rates in 2001 than in 2002 may give an indication of how the annual flow regime influences spawning success in Yellowstone River paddlefish. Although the small number of sample sites may have limited our ability to accurately assess relative spawning effort for both years, our results were consistent with young-of-the-year surveys that indicated reproduction was less successful during the low flow year of 2001 than during 2002 (D. Scarnecchia, University of Idaho, pers. comm.). At this time, it is difficult to determine which aspects of the flow regime (e.g. magnitude or duration of increasing discharge) possibly contributed to the results seen in our study. Wallus (1986) had found a positive relationship between paddlefish reproduction, as evidenced by larval densities, and the magnitude of river discharge during the spawning season. However, Lein and DeVries (1998) detected spawning along the Tallapoosa River, Alabama at peak discharges lower than previously reported. Others have implicated rapidly fluctuating flows in the low levels of spawning activity and reproductive success observed in populations of paddlefish (Hoxmeier and DeVries 1997; Lein and DeVries 1998) as well as sturgeon (Khoroshko 1972; Auer 1996). Fluctuating discharge may contribute both to a low number of migrating adults (i.e. low spawning potential) as well as to a diminished spawning response resulting in substantial resorption of eggs. Moreover, fluctuating, low flows may influence the inundation of spawning grounds and the survival rates of drifting larvae, both of which factor into determining reproductive success.

The objective of this study was to develop a technique that would verify suspect spawning sites rather than estimate the geographical extent of paddlefish spawning grounds along the lower Yellowstone River. However, the success of the egg tubes indicates that they could be used as a management tool to identify the spatial distribution of paddlefish spawning activity. The discovery of an extensive incubation area would support the protection of a greater reach of the lower Yellowstone River. In addition, the continued use of these egg collectors could increase our understanding of the relationship between hydrograph variability and spawning activity. Increasing the number and distribution of sample sites could provide not only a more accurate assessment of the relationship between flow variables and spawning effort, but also would allow inter-annual comparisons between the flow regime and the spatial distribution of spawning paddlefish. This information would further aid management in gauging the impacts of flow manipulations on paddlefish spawning behavior.

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Table 1. General description of the four sites sampled for paddlefish eggs along the lower Yellowstone River during 2000-2002.

Sample site	YRkm[a]	Length of site (km)	Avg. width of site (km)	Sample depth range (m)[b]	Sample site comments
1	9.5	0.35	0.20	1.5 - 4.9	Gravel present in deep channel thalweg along the west bank
2	13.5	0.75	0.35	0.9 - 4.6	Wide mid-channel thalweg; Shallow gravel, rubble shoal located downriver
3	21.5	0.45	0.30	0.9 - 2.5	Shallow gravel, rubble shoal located along the north bank
4	25.5	0.65	0.25	0.9 - 3.8	Shallow gravel, rubble shoal located throughout the upriver segment

[a] Yellowstone River kilometer

[b] Depths varied depending on river stage

Table 2. Effort expended collecting Acipenseriform eggs along the lower Yellowstone River from 2000-2002.

Year	Site	Collectors Deployed	Collectors Retrieved	Collector Days
2000	2	35	31[a]	185[b]
	3	13	10	26
	4	23	18	42
	Total	**71**	**59**	**253**
2001	2	12[c]	3	14
	2	91[d]	88	338
	Total	**103**	**91**	**352**
2002	1	50	48	176
	2	114	111	412
	Total	**164**	**159**	**588**

[a] Three collectors retrieved during mid-summer after initial attempts failed

[b] Includes 103 d from the 3 collectors retrieved in mid-summer

[c] Long tubes

[d] Short tubes

Table 3. Acipenseriform egg collection information for tubes deployed along the lower Yellowstone River in 2001 and 2002. Confirmed indicates number of eggs genetically identified as paddlefish at the National Fish and Wildlife Forensics Laboratory in Ashland, OR.

Year	Site	Sample Period	Collectors Retrieved	Collectors w/ Eggs (%)	Range of eggs per collector	Total eggs (Confirmed)	CPUE[a]
2001	2	May 18-21	3[b]	0(0)	--	0	0.00
		May 28-31	15	0(0)	--	0	0.00
		May 31-June 4	14	0(0)	--	0	0.00
		June 4-8	15	0(0)	--	0	0.00
		June 8-12	15	2(13)	2-5	7(5)	0.12
		June 12-17	15	1(7)	1	1(1)	0.01
		June 19-22	14	6(43)	1-2	9(8)	0.21
		Total	**91**	**9(10)**		**17(14)**	
2002	1	May 24-27	12	0(0)	--	0	0.00
		May 30-June 3	6	0(0)	--	0	0.00
		June 8-13	6	5(83)	1-6	14(10)	0.47
		June 13-17	6	3(50)	3-4	11(8)	0.46
		June 17-21	6	1(17)	6	6(1)	0.25
		June 21-25	6	2(33)	1-2	3(0)	0.13
		June 25-27	6	0(0)	--	0	0.00
		Total	**48**	**11(23)**		**34(19)**	
	2	May 24-27	12	0(0)	--	0	0.00
		May 27-30	15	1(7)	1	1(1)	0.02
		May 30-June 3	15	0(0)	--	0	0.00
		June 8-13	14	7(50)	1-4	16(10)	0.23
		June 13-17	13	10(77)	1-12	34(28)	0.65
		June 17-21	15	6(40)	1-11	18(10)[c]	0.30
		June 21-25	14	2(14)	1	2(2)[d]	0.04
		June 25-27	13	0(0)	--	0	0.00
		Total	**111**	**26(23)**		**71(51)**	

[a] CPUE is number of eggs per collector per sample period duration

[b] Long tubes used during this sample period

[c] One egg genetically identified as *Scaphirhynchus* sp.

[d] Eight additional eggs (5 confirmed as paddlefish) found on a recovered mat deployed in 2000

Table 4. Results of model selection analysis for negative binomial models that describe the distribution of Acipenseriform eggs found on collectors retrieved along the thalweg at sites 1 (n=17) and 2 (n=31) along the Yellowstone River from June 8 to 25, 2002. Numerical and lettered subscripts indicate mean (*m*) and dispersion (*k*) parameters specific to site and time period, respectively. Parameter *b* indicates the estimated time period after which egg counts linearly decreased to 0. AIC difference (Δ_i) indicates the difference between the model's AIC and the best model's AIC (176.5). The subset of best approximating models included those where Δ_i was ≤ 2.

Model	Estimated parameters	Number of parameters	AIC difference	Parameter values for set of best approximating models[c]
1	$m_{1a},\ldots,m_{1d}$, $m_{2a},\ldots,m_{2d}$, k_1, k_2	10	13.52	
2	$m_{1a},\ldots,m_{1d}$, $m_{2a},\ldots,m_{2d}$, k	9	11.22	
3	$m_a,\ldots,m_d$, k_1,k_2	6	3.77	
4	$m_a,\ldots,m_d$, k	5	1.88[b]	2.08, 3.55, 1.75, 0.42, 0.92
5	m_1, m_2, k_1, k_2, b	5	3.33	
6	m_1, m_2, k, b	4	2.35	
7	m, k_1, k_2, b	4	0.9[b]	2.47, 1.76, 0.63, 2
8	m, k, b	3	0[a]	2.44, 0.82, 2
9	m_1, m_2, k_1, k_2	4	8.76	
10	m_1, m_2, k	3	7.81	
11	m, k_1, k_2	3	6.40	
12	m, k	2	5.55	

[a] best approximating model

[b] substantial support for being the best approximating model

[c] values listed in the same order as in 'Estimated parameters' column

Figure 1. Map of the study area

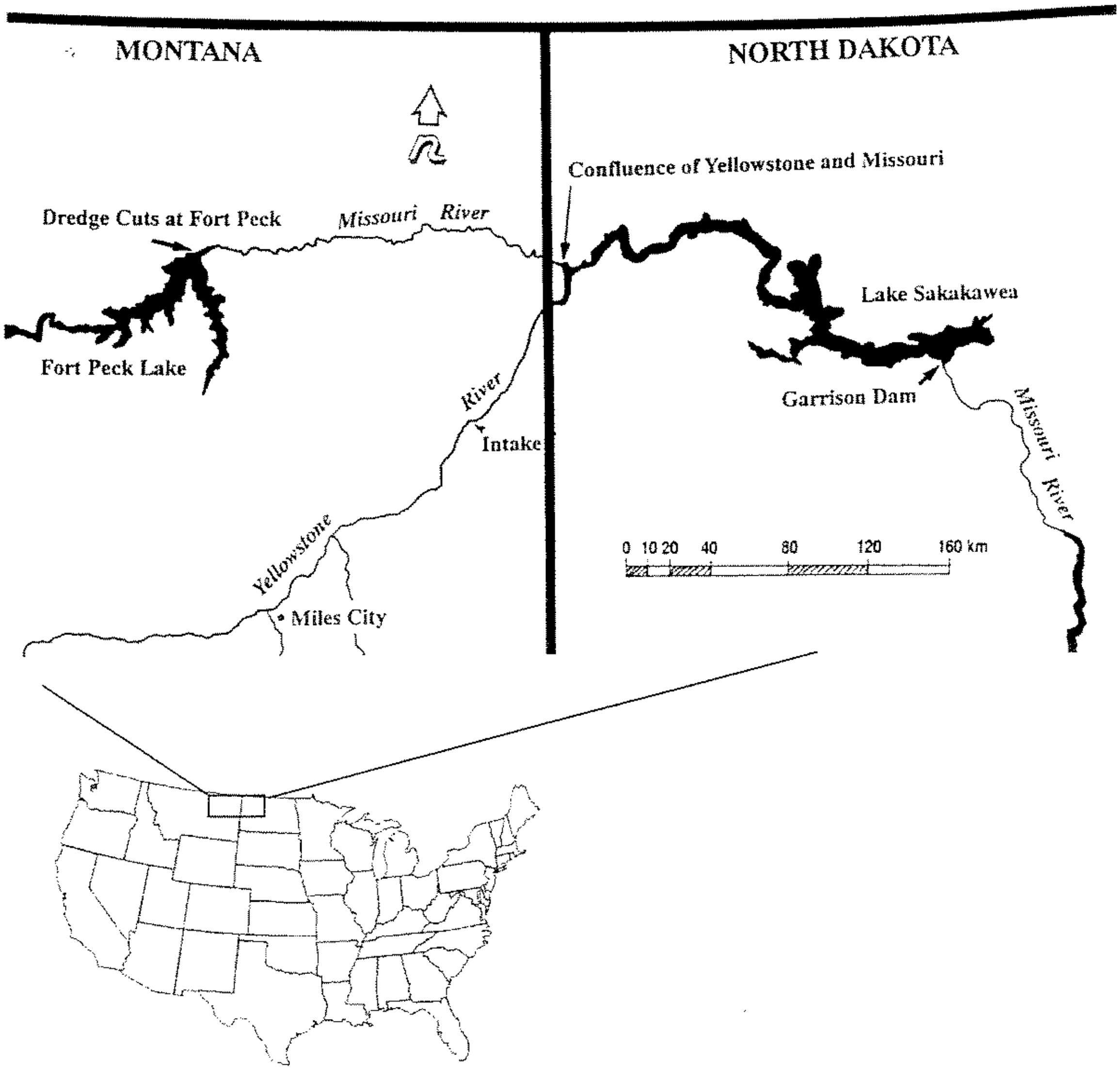

Figure 2. Map of the lower Yellowstone River indicating the river kilometers (rkm) where eggs were sampled during 2000-2002. The rectangular box on each aerial photo designates the area in which egg collectors were deployed; stippled area indicates the location of gravel/rubble shoals within sample sites. Distance scale applies to the aerial photos.

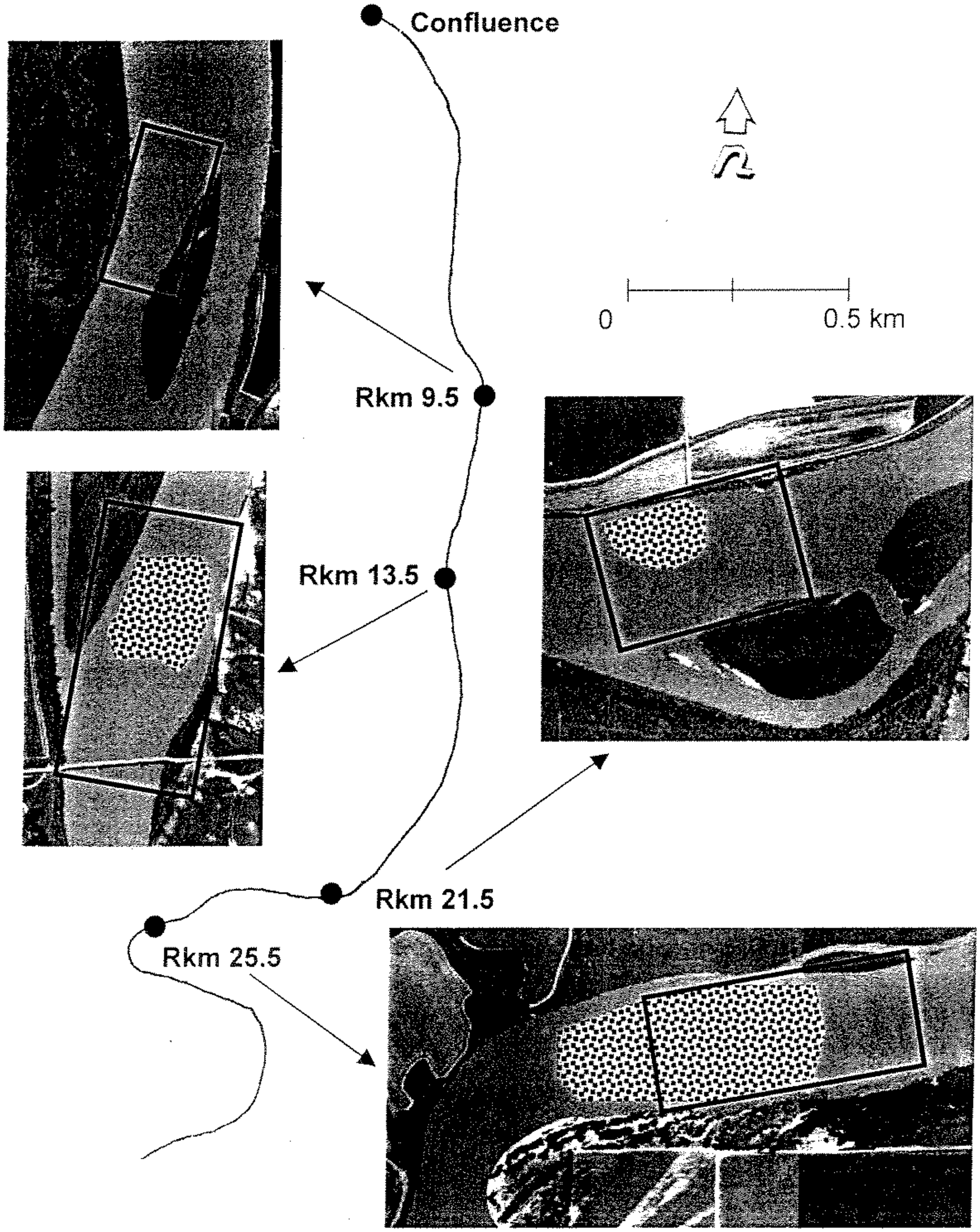

Figure 3. Diagram of the short tubes used to collect eggs along the lower Yellowstone River in 2001 and 2002.

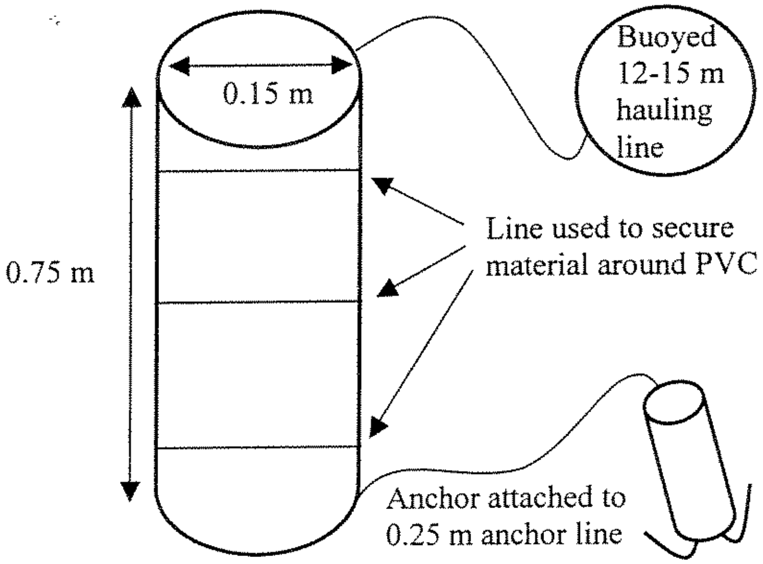

Figure 4. Temporal trends of egg CPUE at sample sites in relation to Yellowstone River variables during 2001 and 2002. The number of symbols along the horizontal CPUE bar indicates the duration of the sampling period in days.

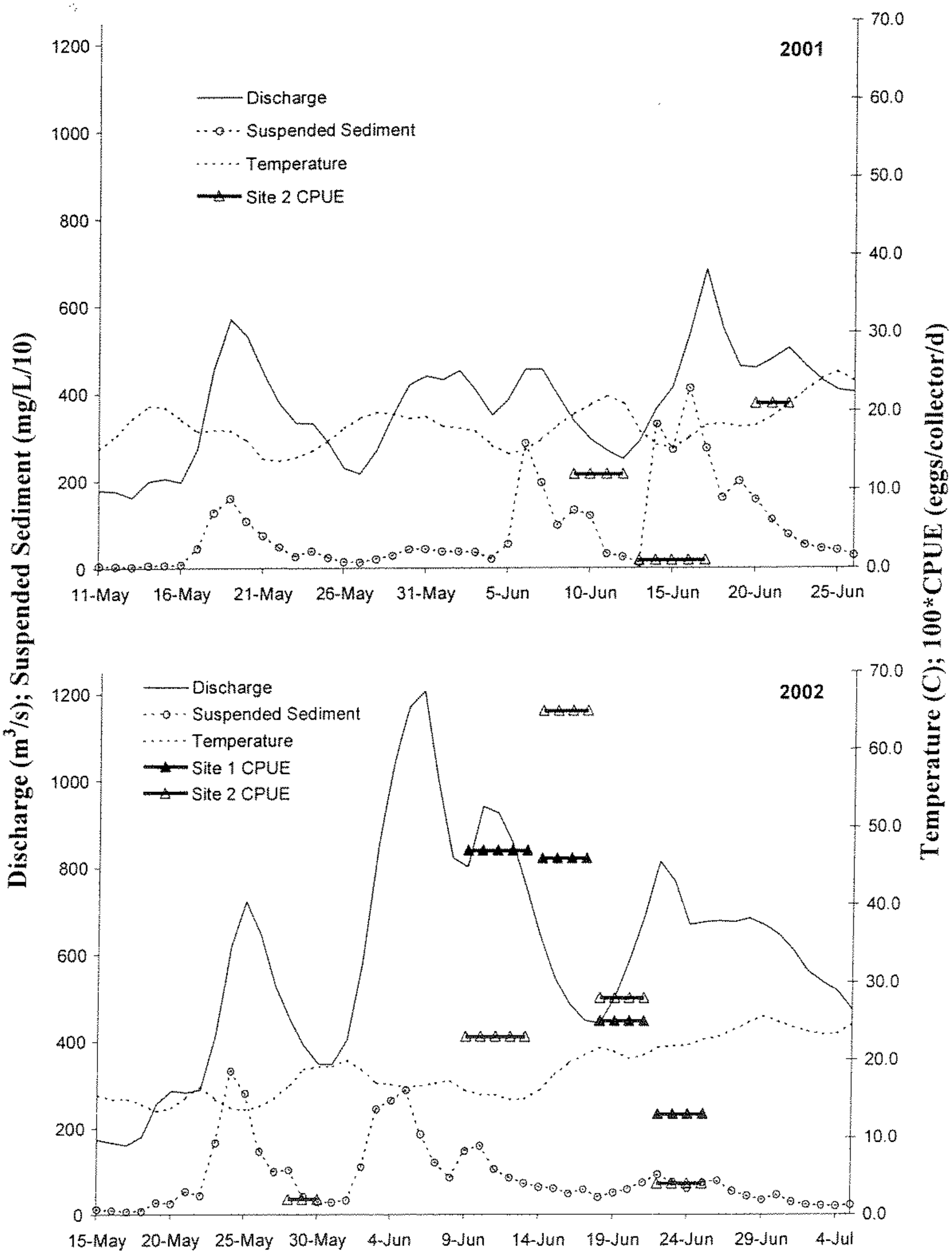

Figure 5. Depth distribution of the short tubes retrieved and those retrieved with eggs from both lower Yellowstone River sites during June 8-25, 2002.

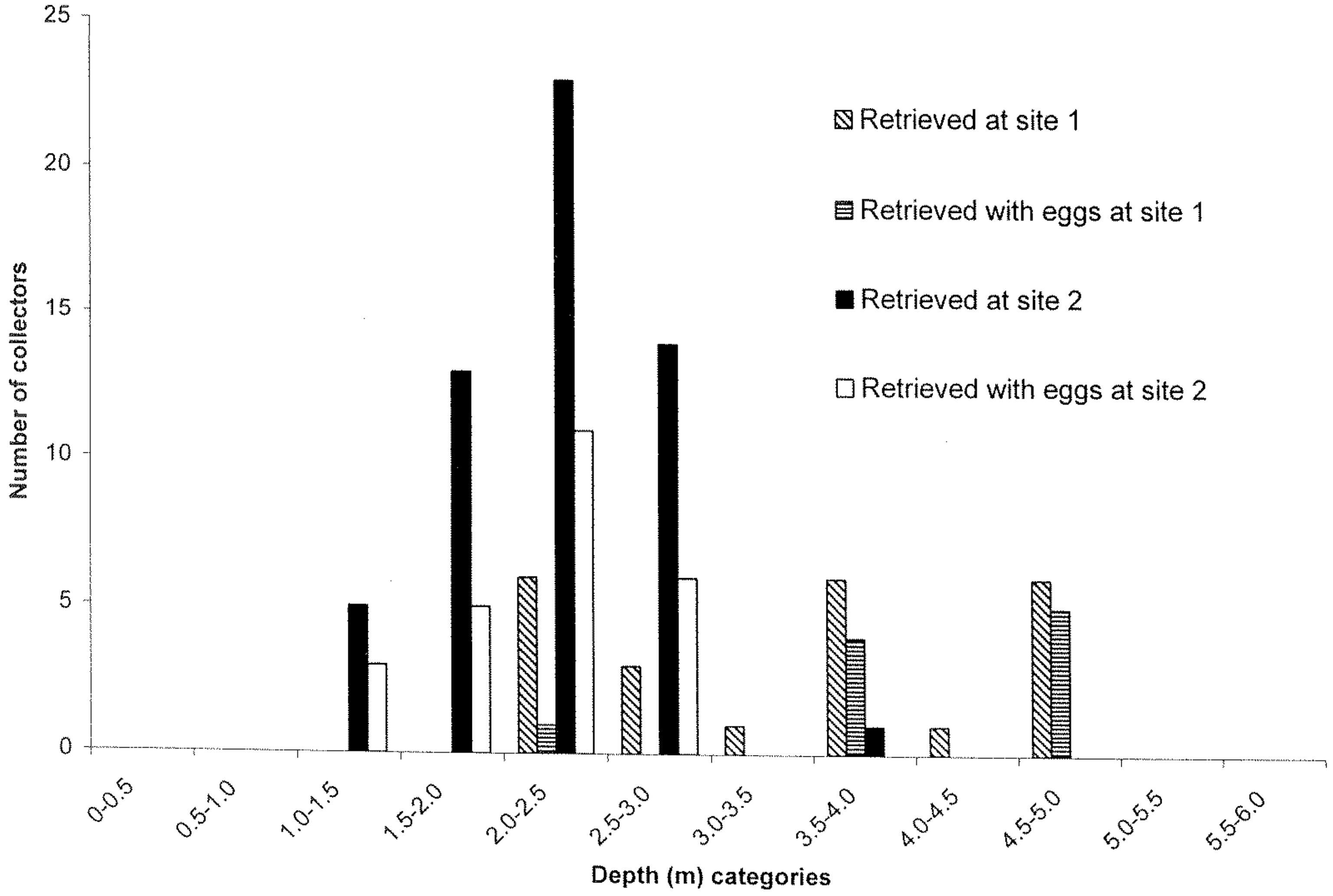

Figure 6. Distribution of Acipenseriform eggs found on short tubes retrieved from both lower Yellowstone River sites during June 8-25, 2002. Solid and hatched fill within the vertical bars indicate the number of collectors retrieved from within and without the channel thalweg, respectively.