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MULTI-SCALE PERSPECTIVES ON PADDLEFISH POPULATIONS:
IMPLICATIONS FOR SPECIES CONSERVATION AND MANAGEMENT

by

Brenda May Pracheil

A DISSERTATION

Presented to the Faculty of
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MULTI-SCALE PERSPECTIVES ON PADDLEFISH POPULATIONS:
IMPLICATIONS FOR SPECIES CONSERVATION AND MANAGEMENT

Brenda May Pracheil, Ph.D.

University of Nebraska, 2010

Adviser: Mark A. Pegg

The Order of fishes containing paddlefish and sturgeon has been named the most endangered group of organisms on the planet by the International Union of Conservation of Nature (IUCN). Population trajectories of paddlefish, whose native range is entirely encompassed within the United States of America, are currently unknown, although the IUCN has considered them to have a high extinction risk in the wild. The declaration of the vulnerability of paddlefish to extinction, coupled with the global plight of other sturgeon species create urgency to establish population and species-level population trajectories. Moreover, this declaration creates a great need for swift management and conservation plans to prevent further species decline and loss. In this dissertation, I use multi-scale analyses ranging from local (Nebraska and South Dakota) to nearly range-wide (all states except Montana and North Dakota) to examine paddlefish population dynamics, and movement.

For Simon and Norah

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CHAPTER 1: INTRODUCTION

Global freshwater biodiversity is experiencing rapid declines (Dudgeon 2006; Jelks et al. 2008). Large rivers, in particular, have seen tremendous declines in biodiversity at the hands of alterations that change natural flow regimes (Dudgeon et al. 2006; Vorosmarty et al. 2010). Consequently, riverine biota that capitalize on elements of natural flow regimes to complete their life cycles have suffered declines due to loss of spawning cues, spawning and nursery habitat, and blocking of seasonal migration routes (Poff et al. 1997; Lytle and Poff 2004).

Declines have been particularly precipitous for migratory fishes including some of the most evolutionarily primitive fishes that have existed virtually unchanged in rivers for millions of years. The systems these primitive fishes have adapted in are characterized as having high natural variability in the annual and seasonal disturbance regimes that many primitive fishes need to complete their life cycles. The Order Acipenseriformes (paddlefish and sturgeon), for example, has now become critically threatened on a global scale in the face of riverine alterations and the International Union of the Conservation of Nature (IUCN) has recently named this Order the most endangered group of species on the planet. Only three of the 28 species in this Order are listed by the IUCN as species of least concern (taxa are abundant in the wild), and the remaining 25 species are at some risk of extinction in the wild. Losses sustained as a result of habitat alteration are also coupled to losses sustained due to overharvest and poaching for caviar. This Order faces continued future threats to population stability due to the collapse of several sturgeon

caviar fisheries that will place greater harvest pressure on a decreasing group of stable species.

The North American paddlefish *Polyodon spathula*, a warm-water potamodromous fish species native to the Mississippi River basin of the USA, has experienced population declines throughout its range for the better part of the last century (Gengerke 1986). Declines in paddlefish populations are largely attributed to anthropogenic alterations to rivers where paddlefish live; alterations that have created conditions incompatible with several aspects of their life history (Jennings and Zigler 2009). For instance, dams have blocked spawning migrations (Unkenholz 1986), prohibited access to spawning habitat (Sparrowe 1986; Unkenholz 1986), and altered flow regimes that serve as cues for spawning and other seasonal movements. Additionally, channelization has severed floodplain connectivity limiting access to backwater nursery areas (Graham 1997) also playing a role in paddlefish population decline.

Paddlefish, in particular, face increasing threats from shifting harvest pressures. Future threats to paddlefish will likely come from compensation for loss of valuable sturgeon harvested for caviar such as the beluga sturgeon *Huso huso*—a European sturgeon that has been critically endangered due in part to overharvest. Additionally, less valuable caviar species such as the shovelnose sturgeon *Scaphirhynchus platyrorhynchus* are also federally protected from harvest in parts of their range due to their similarity of appearance to the federally endangered pallid sturgeon *S. albus* thus potentially shifting more caviar harvest pressure onto paddlefish.

Paddlefish are currently listed by the IUCN as a vulnerable species, meaning that it faces a high risk of extinction in the wild, yet its population trend is currently listed as unknown. Therefore, it is critical that progress is made in understanding the trajectories of paddlefish populations at-large to gain insight into their potential responses to anthropogenic alteration, overharvest, and conservation actions. Furthermore, information gained on the response of paddlefish populations at-large may lend valuable insight into how other sturgeons will respond to increasing threats to persistence and can therefore serve as a framework for conservation of sturgeon species at-large.

Understanding responses of paddlefish populations at-large require evaluations from a multi-scale perspective. Specific information gained at local scales can aid in interpretations of regional and range-wide scale results. Long-distance migratory movements; however, require them to frequently traverse boundaries of jurisdictions that currently govern harvest and conservation practices of this species. Knowledge gained about this species at a range of scales is therefore critical to creating policies that can protect and manage this truly interjurisdictional fish.

This dissertation focuses on paddlefish population ecology from a range of scales from local to range-wide to better understand population trends and explore ways that future population declines can be mitigated. I begin this document by examining local effects of how flow of a relatively unaltered tributary and a highly altered mainstem river affect recruitment of a naturally reproducing paddlefish population (Chapter 2). I next explore the local effects of paddlefish stocking as a conservation tool by examining the effects of entrainment and stocking on paddlefish movements (Chapter 3) and qualitative

(e.g., factors affecting recruitment, effects on apparent mortality, and growth) and quantitative (e.g., numeric population response) effects on a naturally reproducing population (Chapter 4). The final research chapter of this dissertation focuses on a range-wide perspective of consistencies between current state-by-state management of this species and movements of individual paddlefish (Chapter 5). Finally, I conclude with recommendations for paddlefish conservation and management 1.) in South Dakota and Nebraska, 2.) this species at-large, and 3.) of fishes of the Order Acipenseriformes using paddlefish as a framework (Chapter 6).

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CHAPTER 2: TRIBUTARIES INFLUENCE RECRUITMENT OF FISH IN LARGE RIVERS

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ABSTRACT

Recent work demonstrates tributary inputs are important community reorganization points for river biota; however, no studies have examined long-term effects of tributary inputs on fish population dynamics. This study examines nearly 40-yr of young-of-year (yoy) paddlefish recruitment data to investigate the hypothesis tributaries influence mainstem fish population dynamics. We generated hydrologic variables from daily mean flow data (1965 – 2007) from an impounded reach of the mainstem Missouri River and from the Niobrara River, a relatively unaltered tributary, using Indicators of Hydrologic Alteration software. Three multiple regression models using natural-log transformed catch per unit effort (logcpue) as the response variable were created using 1) Missouri River only flow variables, 2) Niobrara River only flow variables, and 3) Missouri River and Niobrara River flow variables. Flow variables from the Niobrara River explain a greater proportion of yoy paddlefish logcpue variability demonstrating that tributaries can positively impact fish population dynamics in altered rivers.

INTRODUCTION

The ecological importance of tributaries on mainstem rivers has largely been overlooked in the underpinning concepts of river ecosystem restoration. The river continuum concept, for example, predicts a continuum of change in species diversity and nutrient availability of rivers as stream order increases (Vannote et al. 1980). While this concept considers the average effect of tributaries on a river system, the local impacts incurred by receiving tributary input may be much greater than that predicted by the river continuum concept. Moreover, the flood pulse concept (Junk et al. 1989) and the riverine productivity model (Thorpe and DeLong 1994), do not specifically account for flow and nutrient additions from tributaries into an altered mainstem river that may attenuate effects of river alteration. Recent findings indicate that tributary inputs cause abrupt local changes in river geomorphology and biodiversity that interrupt the ecologic continuum of the mainstem (Rice et al. 2001). Investigation of 167 tributary-mainstem confluences showed tributaries create sudden changes in mainstem geomorphology including increases in channel complexity, changes in substrate composition, and increased pool depth (Benda et al. 2004). These geomorphic changes increase habitat complexity near tributary-mainstem confluences and have been linked to increases in mainstem diversity downstream of tributaries (Fernandez et al. 2004).

The use of relatively unregulated tributaries to mitigate adverse effects of mainstem river alteration, particularly the effects of river impoundment, has recently been forwarded as a new strategy for river ecosystem restoration (Moyle and Mount 2007). Tributaries of large rivers maintaining elements of their natural flow regime,

predominantly in the case of tributaries to altered mainstem rivers, have been found to be critical to the success of many native river fish species. Successful spawning by humpback chub *Gila cypha*, for example, is dependent on individuals migrating from the highly altered Colorado River near Grand Canyon, Arizona, into a relatively unaltered tributary containing necessary spawning habitats and hydrologic conditions (Gorman and Stone 1999). Similarly, adult paddlefish *Polyodon spathula* migrate up the relatively unregulated Yellowstone River from the Missouri River to spawn (Firehammer and Scarnecchia 2005). Presumably the more natural flow regime of the Yellowstone River yields better spawning habitat than available in the more altered Missouri River (Firehammer and Scarnecchia 2005). This biological interaction between tributary and mainstem rivers also likely impacts fish population and community dynamics. Several studies have shown a high degree of interconnectedness between mainstem and tributary fish populations such as channel catfish *Ictalurus punctatus* (Dames et al. 1989), blue sucker *Cycleptus elongatus* (Neely et al. in press), paddlefish (Firehammer and Scarnecchia 2005), and pallid sturgeon *Scaphirhynchus albus* (Snook et al. 2002).

Understanding the relative influences of tributaries to their mainstem rivers may yield a greater understanding of river ecosystems that can aid in effective recovery plans. Some linkages between tributaries, altered mainstem rivers, and fish populations have been made, but long-term empirical assessments of the impacts of tributaries on mainstem fish population dynamics are absent from the literature. Here we examine a nearly 40-yr data set to evaluate the long-term relative influences of a tributary and a mainstem river on fish population dynamics. We investigate the hypothesis that a tributary can provide measurable contributions to a mainstem fish population using

young-of-year (yoy) paddlefish recruitment in a reach of the impounded Missouri River. Specifically, we predicted that there would be an unequal effect of flow from the mainstem Missouri River and the Niobrara River on yoy paddlefish recruitment due to differing degrees of alteration for each river.

STUDY AREA

The Missouri River portion of the study area is a 111-km reach bounded on the upstream end by Ft. Randall Dam and downstream by Gavins Point Dam (Figure 2.2.1) with the Niobrara River being the only major tributary in this reach. Lewis and Clark Lake, an impoundment of the Missouri River is formed by Gavins Point Dam, is the smallest and downstream-most of the six dams on the mainstem Missouri River. Ft. Randall Dam is a power-peaking hydropower facility that creates daily downstream water-level fluctuations of >1-m in the summer months (Hesse and Mestl 1993). Gavins Point Dam and Ft. Randall Dam were in place during the entire study period: construction of Gavins Point Dam was completed in 1955 and construction of Ft. Randall Dam was completed in 1953.

The Niobrara River (Figure 2.2.1) extends 692-km from its headwaters in Wyoming to its confluence with the Missouri River near Niobrara, NE. This river maintains many elements of its natural flow regime including a period of high spring flows that occur between mid-February and mid-June. Spencer Dam, the downstream most of the four dams on the Niobrara River, is a run-of-the-river (uncontrolled flow) hydropower generating dam completed in 1927 approximately 62-km from its confluence with the Missouri River. Hydrographs of hourly discharge data from the Niobrara River at Verdel, NE gauging station maintained by the United States Geological Survey (about

23-km upstream of the confluence of the Niobrara and Missouri rivers) indicate that there is very little diel fluctuation in water levels.

MATERIALS AND METHODS

Dependence of paddlefish on a number of flow-related attributes for life-cycle completion (Russell 1986) makes yoy paddlefish recruitment a good indicator of the relative ecologic effects of mainstem and tributary flows. Young-of-the-year paddlefish have been collected in the same reach of the Missouri River downstream of the Niobrara River confluence, nearly every year from 1965 to the present. This data set allows us to quantify the relative long-term influences of tributary and mainstem flow on yoy paddlefish recruitment between two dams, Ft. Randall Dam and Gavins Point Dam, on the Missouri River.

Fish Collection

Weekly sampling of yoy paddlefish from June through mid-August occurred annually from 1965-2007 (except 1982-1985 and 1993-1994) in the same location in Lewis and Clark Lake. Sample sites were located within the pre-impoundment Missouri River channel. Collections were made using an 8.2-m otter trawl with 1.9-cm bar mesh and a 0.6-cm cod liner. Sampling consisted of three, 10-min net tows on the reservoir bottom at approximately 10-m of water. Catch per unit effort (cpue) of yoy paddlefish was calculated as fish per minute each year.

Hydrologic analyses

We used mean daily discharge data recorded by the United States Army Corps of Engineers at Ft. Randall Dam and Gavins Point Dam and mean daily discharge data recorded on the Niobrara River from the Verdel, NE gauging station from 15 Oct 1965 –

14 Oct 2007. We summarized flow data using Indicators of Hydrologic Alteration (IHA) software (Richter et al. 1997). This software is based on the range of variation approach (RVA) (Richter et al. 1997) to summarize daily discharge data into ecologically-meaningful hydrologic statistics that describe flow magnitude, timing, duration, frequency, and rate of change for a specified period of time (Richter et al. 1997).

We defined a water year as the period between 15 Oct to the following 14 Oct. Each water year was separated into three seasons based on hydrologic patterns of the Niobrara River: 15 Oct- 14 Feb (winter), 15 Feb- 14 June (spring), 15 June- 14 Oct (summer). The Niobrara River was used to select dates to define seasons because its hydrograph is relatively unaltered compared to the mainstem Missouri River and is believed to retain many of the characteristics believed to be typical of the natural hydrograph in the region. Pre-alteration discharge data is not available for the Niobrara River and is, therefore, not shown. Extreme flow events (high and low flow) were defined by the non-parametric default settings within IHA (the highest and lowest 10% of flows in a season). Specifically, we used the IHA generated variables 1, 3, 7, 30, and 90-d minimum and maximum flows, numbers of high and low flow periods, rate of flow rise and fall, number days of high and low flow, and number of flow reversals (number of changes from ascending to descending hydrograph, and vice versa) for each season in our analyses. We also used monthly mean discharges for a season to determine seasonal mean flow.

Data analyses

Catch per unit effort of yoy paddlefish was ln-transformed to achieve normality. We then correlated ln-transformed cpue (logcpue) with variables generated by IHA

analyses. Continuous variables that were correlated with logcpue at $P < 0.05$ were included in further analyses. Multiple correlations were used only to determine the flow variables that were correlated with logcpue for model inclusion and not as a final measure of association; thus, Bonferroni adjustments were not used to lower the α -value.

Multiple regression models were constructed with all significantly correlated variables to generate models that examined yoy paddlefish recruitment success with response to Niobrara River flows, Missouri River flows, and Niobrara River and Missouri River flows. All variables included in these models were examined for multicollinearity through variance inflation factor (VIF) assessment. All variables with a $VIF > 10$ were removed from the model, removing variables with the highest VIF first (Chatterjee et al. 2000). Stepwise multiple regression was then used to determine the most influential flow variables. Durbin-Watson first-order autocorrelation statistics were generated to identify models with serial autocorrelation.

RESULTS

Daily mean discharge was $699 \text{ m}^3/\text{s}$ from Ft. Randall Dam, $48 \text{ m}^3/\text{s}$ from the Niobrara River near Verdel, Nebraska (approximately 23 km upstream of the confluence with the Missouri River), and $914 \text{ m}^3/\text{s}$ from Gavins Point Dam for the study period (15 October 1965- 14 October 2007). High flow periods did not coincide on the Niobrara River and Missouri River during the study period. For example, the Niobrara River maintained relatively low winter and summer flows and high spring flows while the Missouri River maintained relatively high summer and winter flows and low spring flows (Figure 2.2). Timing of spring high flow events on the Niobrara River during the study

period was similar to the timing of spring high flow events on the Missouri River from 1930-1950, although the Niobrara River spring pulse was not bimodal.

Catch per unit effort of yoy paddlefish ranged from 0.02 - 1.11 with a median cpue of 0.17 (Figure 2.3a). A greater number of flow variables generated from Niobrara River discharge data were significantly correlated with logcpue than flow variables from Missouri River discharge data (Table 2.1). Two of the six variables generated from Missouri River release data were negatively correlated with logcpue whereas four of the 15 variables generated from Niobrara River data were negatively correlated with logcpue.

The suite of Niobrara River variables correlated with logcpue were better predictors of the flow regime than the suite of Missouri River variables correlated with logcpue. For example, Niobrara River flow variables from the spring season described flow magnitude, duration, periodicity, and rate of change while spring flow variables from the Missouri River were descriptive of only flow magnitude and duration. Similarly, Niobrara River winter and summer season flow variables were descriptive of flow magnitude, duration, and periodicity; whereas Missouri River winter variables described flow magnitude and duration but summer variables had no relation with logcpue. No IHA generated variables from Missouri River discharge at Gavins Point Dam were significantly correlated with logcpue and, therefore, will not be discussed further.

Flow variables from the Niobrara River described more variability in yoy paddlefish recruitment than the Missouri River flow despite the Niobrara River having substantially lower discharges. For instance, multiple regression models constructed with only Niobrara River variables explained more variability in logcpue than models

constructed with only Missouri River variables (Table 2.2). Furthermore, when independently considering Niobrara River and Missouri River flow, the variables in the Niobrara River model are characteristic of successful paddlefish reproduction and recruitment. The Niobrara River model (Figure 2.3b), for example, contained only spring flow variables describing natural flow conditions (e.g., spring high flows) that likely serve as paddlefish spawning cues. The Niobrara River spring flow variables are positively correlated with logcpue thus relating a greater number of spring high flow periods and greater spring 7-d minimum flow with greater yoy paddlefish production. The Missouri River model, on the other hand, contained one winter and one spring flow variable (Figure 2.3c). The negative relation between logcpue and winter flow reversals relates a greater number of winter flow reversals from Ft. Randall Dam to fewer yoy paddlefish produced that year. The positive relation between logcpue and spring 1-d minimum flow relates higher spring minimum flows to greater yoy paddlefish production.

The model containing both Niobrara River and Missouri River flow variables (Figure 2.3d) explained the greatest amount of variability in logcpue of the three generated models (Table 2.2) and further demonstrated the relative importance of tributary flows to yoy paddlefish abundances. Both of the two Niobrara River variables in the combined model had larger β -values than the one Missouri River variable, thus suggesting a larger relative influence of the Niobrara River flow regime (Table 2.2). The Niobrara River spring number of high flow periods, again, had a positive association with logcpue linking the increased frequency of spring high flow periods to higher yoy paddlefish recruitment. The only variable in the combined Niobrara River-Missouri

River model that did not appear in either the Niobrara River only or Missouri River only model was the Niobrara River variable summer number of low flow periods. This variable is negatively associated with logcpue, thus suggesting that a greater number of summer low flow periods from the Niobrara River leads to fewer yoy paddlefish produced. The types of variables from the Niobrara River and Missouri River in the multiple regression models also differed. The Niobrara River variables described flow events while the one Missouri River variable was a measure of discharge and reflected water management schemes.

DISCUSSION

The influence of Niobrara River flow on yoy paddlefish recruitment suggests that tributary flow attributes can have an influence on mainstem river fish populations, despite substantially smaller average discharge. The Niobrara River, for instance, has a mean annual discharge 14 times smaller than the Missouri River. The multiple regression model containing only Niobrara River flow variables described more variability in yoy paddlefish logcpue than the model containing only Missouri River flow variables. Therefore, variability in yoy paddlefish logcpue described by the Niobrara River is likely attributed to the dependence of paddlefish on natural flow attributes such as high spring flows to complete their life cycle (Russell 1986). The Niobrara River still maintains several elements of its natural flow regime important to paddlefish reproductive success, such as a magnitude, rate of change, periodicity, and duration of the spring high flow period (Table 2.1). The elements of the natural flow regime retained by the Niobrara River potentially allow paddlefish downstream of the Niobrara River-Missouri River confluence to use spring flow increases as a spawning cue (Russell 1986) thereby moving

to more hospitable nursery habitats near the Niobrara River with greater nutrient availability (Martin and Novotny 1975). The negative correlation between yoy paddlefish abundance and summer flows further impresses the importance of Niobrara River contributions. This negative correlation suggests that increases in low flow conditions brought about by factors such as drought, or increased summer water withdraws from the Niobrara River basin through irrigation or municipal use, may be detrimental to paddlefish reproductive success. Nutrient inputs from the Niobrara River have been linked to plankton availability in Lewis and Clark Lake where yoy paddlefish are collected (Martin and Novotny 1975). Therefore, decreased flows from the Niobrara River may result in decreased nutrient inputs into Lewis and Clark Lake resulting in reduced food availability for yoy paddlefish. Regulation of the Missouri River, especially through impoundment, has also likely played a role in exaggerating the importance of summer nutrient inputs from Niobrara River.

The Missouri River in this study area maintains very few of the historical flow characteristics that have likely driven the evolution of paddlefish life-histories. High flow periods on the Missouri River occur in the winter and summer seasons while historically, high flow periods were in the spring (Junk et al. 1989; Galat and Lipkin 2000; Pegg and Pierce 2003). The current homogenized Missouri River flow regime can adversely impact the paddlefish population in this reach by potentially leaving spawning-ready paddlefish without spawning cues and habitat as well as leave larval paddlefish without nursery habitat. Our data also indicate that regulation of the Missouri River hydrograph, specifically through increases in winter flow variability, is detrimental to the paddlefish population. Mechanistically, this negative correlation may be a result of

increased energy expenditure by adult paddlefish in lieu of establishing spawning energy reserves, ultimately leading to decreased yoy paddlefish recruitment. Likewise, reduced spawning energy reserves have been shown to lead to decreased egg mass and fecundity in white crappie *Pomoxis annularis* (Bunnell et al. 2007) and reduced numbers of spawned eggs, lack of egg development, resorption of egg masses or skipped spawning in adult Atlantic cod *Gadus morhua* (Jorgensen et al. 2006).

In a broader context, this study highlights the importance of tributaries to the function of large river ecosystems. This information could be especially valuable for restoration and management of these dynamic systems. Ecosystem services, necessary for successful fish recruitment, such as flow-induced spawning cues, nutrient influx, inundation of nursery habitat, and flow-dependant larval drift, may be at least partially mediated or restored through tributary protection and restoration. Tributary flows can attenuate effects of upstream regulation through unregulated or less regulated inputs. Tributary inputs can, in this way, naturalize the flow regime that can ultimately benefit native fish species (Poff et al. 1997). Little research has evaluated the supporting role of tributaries to large river biota over periods of several decades. However, the disproportionately large impact tributaries may have on mainstem fish populations creates an urgent need for greater study of the ecologic role of tributaries.

Alteration of large rivers (rivers having a drainage area of $>250,000 \text{ km}^2$) has caused the decline of many fish populations (Hesse et al. 1989; Galat et al. 2004). Habitat mitigation on these rivers, although claiming some successes, takes several years to complete and comes at great monetary expense. However, relatively unaltered tributaries of large rivers are likely providing many services to fish populations in altered

systems. The potential wide-use of tributaries by mainstem river fish populations implies that tributaries may fill valuable ecologic roles that highly altered mainstem rivers no longer provide. Additionally, evidence that tributaries of unaltered mainstem rivers are ecologically important for river biota (Rice et al. 2001) suggests that tributaries may have always been important, but knowledge of their importance is only now emerging in the face of river ecosystem degradation. As such, this study underscores the importance of including tributary conservation and restoration in large river ecosystem recovery plans.

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Table 2.1. Flow variables generated from Niobrara and Missouri river 1965-2007 daily mean flow data using Indicators of Hydrologic Alteration software that were significantly correlated with ln-transformed catch per unit effort with correlation r - and p -values shown for each variable. Units of measure for each variable are given where appropriate.

River	Season	Variable	r	P
Niobrara River	Winter	Mean discharge (m^3s^{-1})	0.3341	0.0433
		90 day minimum flow (m^3s^{-1})	0.3365	0.0417
		Number low flow periods	-0.4334	0.0074
	Spring	Mean discharge (m^3s^{-1})	0.4610	0.0041
		1 day minimum flow (m^3s^{-1})	0.3852	0.0186
		3 day minimum flow (m^3s^{-1})	0.4635	0.0039
		7 day minimum flow (m^3s^{-1})	0.5020	0.0015
		30 day minimum flow (m^3s^{-1})	0.5163	0.0011
		90 day minimum flow (m^3s^{-1})	0.3635	0.0270
		90 day maximum flow (m^3s^{-1})	0.3583	0.0294
		Number low flow periods	-0.3726	0.0232
		Number high flow periods	0.5569	0.0003
		Duration high flow (d)	0.3381	0.0407
		Flow rise rate (m^3s^{-1})	0.4598	0.0042
		Flow fall rate (m^3s^{-1})	-0.3506	0.0334
	Summer	1 day minimum flow (m^3s^{-1})	0.3403	0.0393
		3 day minimum flow (m^3s^{-1})	0.3394	0.0399
		7 day minimum flow (m^3s^{-1})	0.3448	0.0366

Table 2.1 cont.

		Number low flow periods	-0.4325	0.0075
Missouri River	Winter	Number high flow periods	-0.3573	0.0300
		Number flow reversals	-0.4640	0.0038
	Spring	1 day minimum flow (m^3s^{-1})	0.4552	0.0046
		3 day minimum flow (m^3s^{-1})	0.4589	0.0043
		7 day minimum flow (m^3s^{-1})	0.4459	0.0057
		30 day minimum flow (m^3s^{-1})	0.3495	0.0340

Table 2.2. Best stepwise multiple regression models for Indicators of Hydrologic Alteration generated flow variables from the Niobrara River (NR), the Missouri River (MR), and both Niobrara and Missouri rivers with model F -value (F), model R^2 (R^2), model p -value (P), and Durbin-Watson first-order autocorrelation value (D-W).

River	Equation	F	R^2	P	D-W
Niobrara River	$y = - 3.39589 +$ 0.13005 spring number high flow periods + 0.00077 spring 7-d minimum flow	9.93	0.3688	0.0004	1.830
Missouri River	$y = - 3.39746 +$ $- 0.03362$ number winter flow reversals + 0.00007 spring 1-d minimum flow	7.18	0.2970	0.0025	1.659
Niobrara River & Missouri River	$y = -2.3817 +$ 0.10375 NR spring number high flow periods – 0.06623 NR summer number low flow periods + 0.00007 MR spring 1-d minimum flow	8.26	0.4288	0.0003	1.862

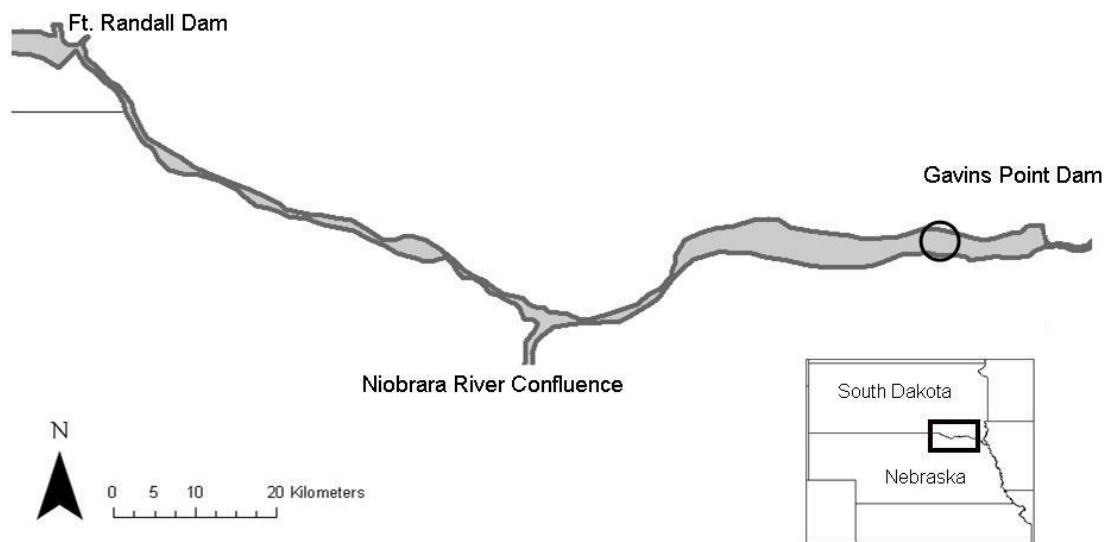


Figure 2.1. The Missouri River between Ft. Randall Dam and Gavins Pt. Dam and the lower Niobrara River. Young-of-year paddlefish were sampled in Lewis and Clark Lake, the reservoir formed by Gavins Pt. Dam including collection site.

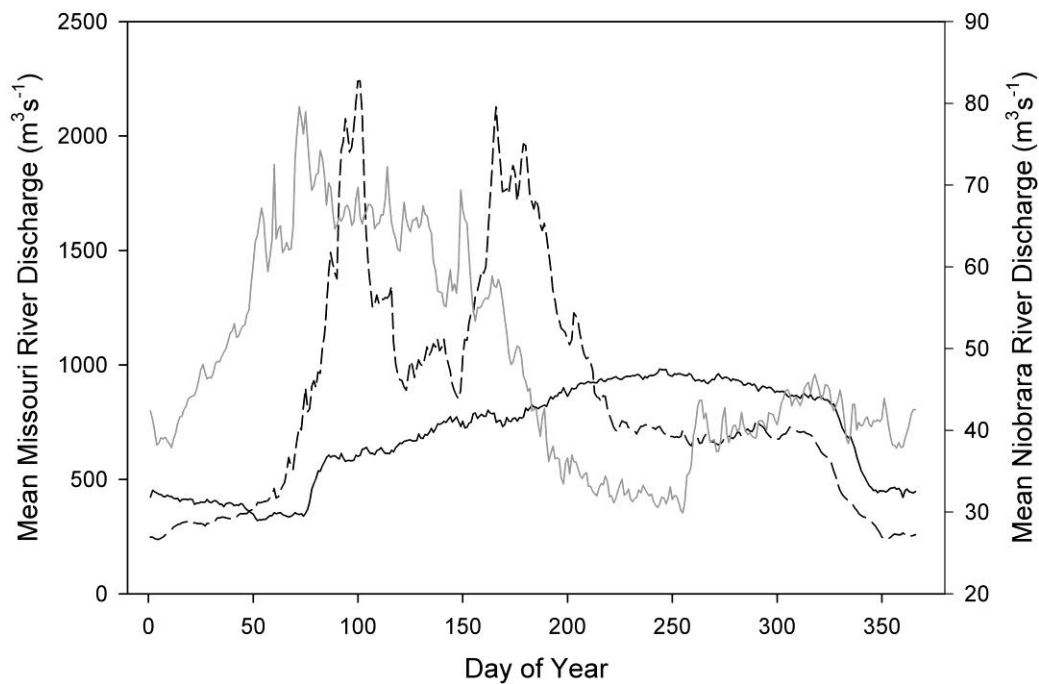


Figure 2.2. Mean of daily mean discharge in m^3s^{-1} (cms) over the study period (1965-2007) from the Niobrara River at Verdel, NE gauge (solid gray line) and Missouri River at Ft. Randall Dam (solid black line). Daily mean flow from the pre-alteration Missouri River (1930-1950) is taken from Yankton, SD (dashed black line).

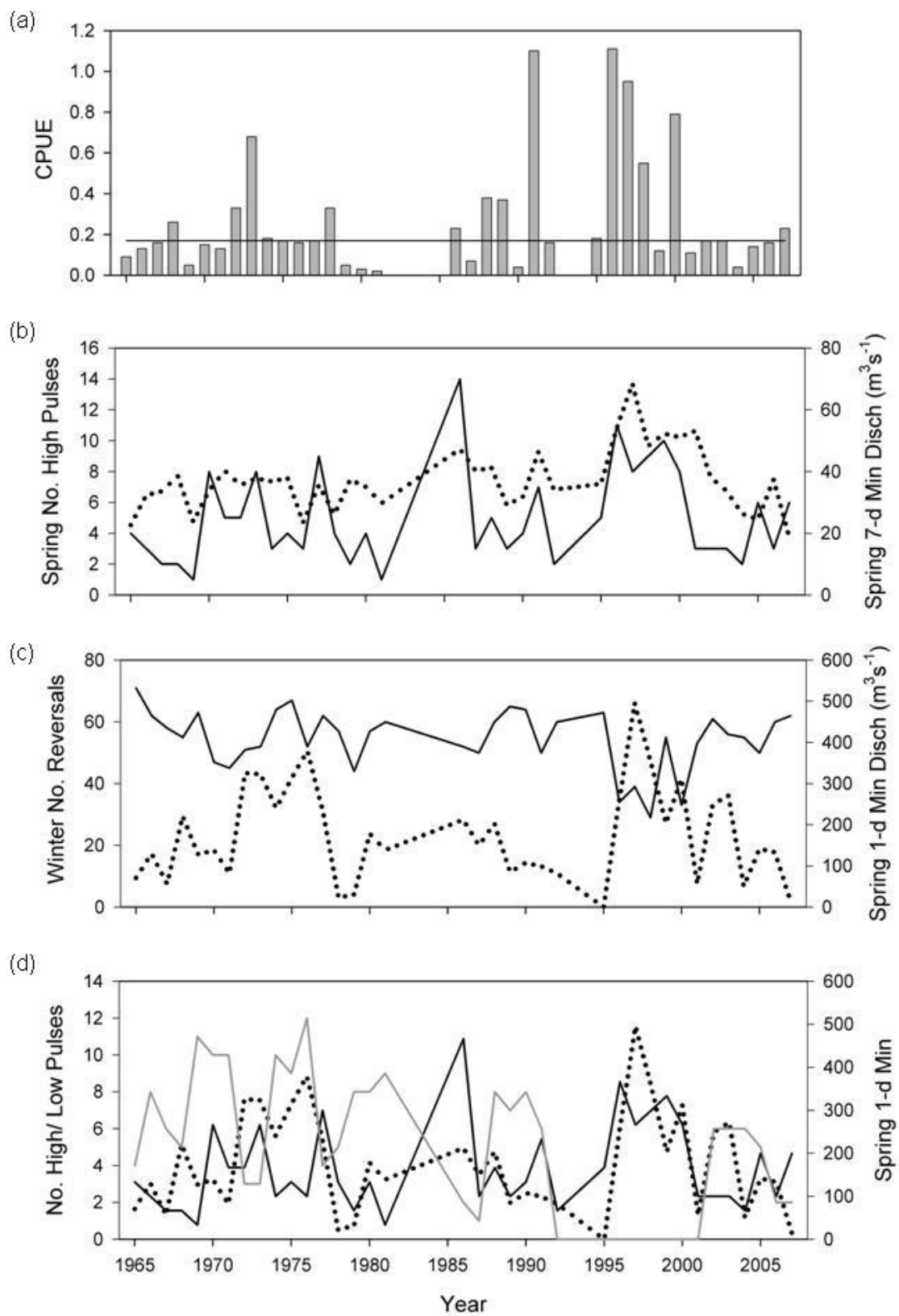


Figure 2.3. Graphical representations of multiple regression equations constructed from Niobrara River and Missouri River flow characteristics used to predict young-of-year paddlefish catch per unit effort (cpue). (a) Annual catch per unit effort (CPUE) in fish*min⁻¹ of young-of-year paddlefish from the Missouri River at Lewis and Clark Lake, 1965-2007 with median cpue of 0.17 (solid black line). (b) Niobrara River only model containing predictor variables spring number of high flow periods (solid black line) and spring 7-d minimum discharge (dotted black line). (c) Missouri River only model containing predictor variables winter number of flow reversals (solid black line) and spring 1-d minimum discharge (dotted black line). (d) Niobrara River and Missouri River combined model containing predictor variables Niobrara River spring number of high flow periods (solid black line) and summer number of low flow periods (solid gray line) and Missouri River spring 1-d minimum discharge (dotted black line).

CHAPTER 3: MOVEMENT AND HABITAT USE OF WILD AND HATCHERY ORIGIN PADDLEFISH: IMPLICATIONS FOR SPECIES RESTORATION

This chapter is in review for publication with coauthors Mark A. Pegg and Gerald E. Mestl

ABSTRACT

Fish species restoration plans often involve stocking hatchery-reared fish. Success of these programs hinges on stocked individuals producing offspring that recruit to adulthood and produce offspring. However, production of young in a supplemented population is dependent on behavioral assimilation of stocked fish into the wild population so they are able to breed with wild fish. We examined movement and habitat use of wild and hatchery origin paddlefish by 1) determining whether average distance moved between relocations differed between wild and hatchery origin paddlefish, including gravid females and 2) determining whether habitat use differed between wild and hatchery origin paddlefish, including gravid females, to determine whether wild and stocked paddlefish had similar behavior. We found that average distance between paddlefish relocations did not differ between wild (13.89 ± 4.73 km) and hatchery (11.48 ± 2.86) origin paddlefish (ANOVA $F_{1,38} < 0.01$; $P = 0.98$) and that habitat use did not differ between wild and hatchery origin paddlefish (ANOSIM; global- $\rho = -0.404$; $P = 0.74$). Likewise, we found that average difference did not differ between wild (0.61 ± 0.19 km) and hatchery (0.51 ± 0.06 km) origin gravid female paddlefish relocations (ANOVA $F_{1,17} = 0.02$; $P = 0.885$) and that habitat use did not differ between wild and hatchery origin

gravid female paddlefish (ANOSIM; global $\rho=0.056$; $P= 0.96$). The results of this study suggest that hatchery origin paddlefish that are stocked as young integrate into the wild population and are behaviorally equivalent to wild paddlefish.

INTRODUCTION

Fish species restoration plans often involve stocking fish with the aim of creating a viable population through integration of wild and stocked individuals. The ultimate goal of stocking is that the integration of the wild and stocked individuals will lead to the natural production of offspring that will recruit to adulthood. Specifically, restoration success hinges on stocked fish behaviorally integrating into the wild population through similar spawning movements, habitat use, etc. so that the introduced individuals can spawn with wild fish. Conversely, sustained segregation of wild and stocked individuals would not allow for integrated spawning and may inhibit the ultimate goal of population viability.

The assumption that fish population trajectories positively respond to restoration stockings is not well-supported by past studies. Disparate movements and behaviors of wild and stocked fish have been frequently reported (see review in Huntingford 2004) potentially upending creation of a viable population through stocking. For example, stocked juvenile chub *Leuciscus cephalus* were found to move greater distances than their wild counterparts over a short time period (Bolland et al. 2008). Differences in behaviors such as movement patterns and habitat use of wild and stocked fish over short study periods have also been reported for several species of salmonids including brook trout *Salvelinus fontinalis* (Vincent 1960), rainbow trout *Oncorhynchus mykiss* (Bjornn and Mallet 1964), and brown trout *Salmo trutta* (Weiss and Schmutz 1999). Several studies

also suggest that certain behaviors of offspring in stocked populations manifest in decreased fitness compared to wild populations thus increasing the need for understanding comparative behaviors between wild and hatchery origin fish. Hatchery origin steelhead trout *O. mykiss* for instance, have been reported to have earlier spawning dates and decreased offspring survival compared to wild origin offspring (Chilcote et al. 1986). Decreased survival of hatchery progeny has been partially attributed to less favorable environmental conditions as spawning date is moved earlier in the year.

There is little evaluation of how stocking young fish translates into behavioral assimilation with the wild population as adults even though most stockings are of young fish. Additionally, there is no evaluation of how stocking young fish behaviorally translates to adults in the case of long-lived, late-maturing fish. Evaluation of comparative behaviors between wild and hatchery-origin fish is especially important for long-lived, late maturing fish species because many of these species have experienced drastic population declines over the last century (Graham 1997; Jennigns and Ziegler 2000). Furthermore, as stocking becomes increasingly critical to restoration plans for long-lived, late maturing fish species, a greater understanding of the effects of stocking is imperative to protecting these fishes.

We examined differences in movements and habitat use of wild and hatchery-reared paddlefish *Polyodon spathula* to gain insight on the potential impacts for different behaviors of stocked versus wild long-lived fish. Paddlefish are good candidates to address this question because they are a long-lived, late maturing fish species that has been reported to live >50 years and mature at 8-12 years of age (Graham 1997). Paddlefish have been frequently stocked throughout the Mississippi River Basin, in many

cases, to compensate for population declines (Graham 1997) and to increase the adult population that can contribute offspring to the population. Several studies have been conducted on movements of young paddlefish post-release (Pittman and Parks 1994; Rouch et al. 2003; Barry et al. 2007) and several studies have also investigated movements of wild paddlefish (Southall and Hubert 1984; Moen et al. 1992; Lien and DeVries 1998; Zigler et al. 1999; Paukert and Fisher 2001; Stancill et al. 2002; Zigler et al. 2003; Zigler et al. 2004; Firehammer and Scarnecchia 2006; Firehammer and Scarnecchia 2007; Miller and Scarnecchia 2008), but there has been no contemporaneous comparison of movements of adult wild and hatchery-origin paddlefish.

We evaluated movements and habitat use of wild and hatchery origin paddlefish to assess their behavioral equivalence. All hatchery origin paddlefish were stocked as age-0 individuals and have had several years (≥ 12 years, in most cases) to acclimate to the natural environment. We examined movement and habitat use of the wild and hatchery origin paddlefish in this study by determining 1) whether average distance moved between relocations differed between wild and hatchery origin paddlefish, and 2) whether habitat selection differed between wild and hatchery origin paddlefish.

STUDY AREA

The study area was a 111-km reach of Missouri River on the border of Nebraska and South Dakota, USA, bounded on the upstream end by Ft. Randall Dam (forming Lake Francis Case) and downstream by Gavins Point Dam (forming Lewis and Clark Lake) (Figure 3.1). The Niobrara River is the only major tributary in the study area. The study area was divided into 4 segments with distinct fluvial geomorphic features: Tailwater—the segment adjacent to Ft. Randall Dam that is immediately impacted by the

impoundment; Riverine—a sediment-poor, degrading segment of river immediately downstream of the Tailwater segment; Delta—formed by confluence with the Niobrara River and characterized as having an aggrading river channel with high sediment loads and channel complexity; and Reservoir—area of impounded water formed by Gavins Point Dam. The reservoir segment had the largest area and the tailwater segment had the smallest area (Table 3.1).

MATERIALS AND METHODS

Paddlefish Collection and Telemetry

Paddlefish were captured using 183 x 2-m floating gill nets with 8-cm bar mesh (in Ft. Randall Tailwater and Lewis and Clark Lake), 46 x 2-m floating trammel nets 8-cm bar mesh (throughout the study area), 91 x 4-m boat-deployed seine with 1-cm mesh (in Ft. Randall Tailwater); 91 x 4-m 2-cm mesh surface trawl (in Lewis and Clark Lake). We attempted to implant transmitters in paddlefish from throughout the study area; however, we were only able to capture paddlefish in Ft. Randall Dam tailwater and Lewis and Clark Lake. Paddlefish were weighed and measured (eye-to-fork length) upon capture and gender was determined when possible. Age and stocking location was determined for hatchery-origin fish through decoding coded wire tags implanted just prior to stocking. Age was not determined for wild paddlefish because paddlefish jaws are used for aging and jaws cannot be collected without euthanizing the fish.

Paddlefish >1000 mm and >18 kg (most likely to be gravid females; Stastny 1992) were preferentially implanted with transmitter tags to gain insights into spawning behavior; however, paddlefish of unknown sex and maturity were also implanted with transmitters. Paddlefish were implanted with 2 models of Lotek (Newmarket, Ontario,

Canada) combined hybrid SRX radio/ MAP acoustic tags: 15 fish (6 wild and 9 hatchery) with CH32-50 tags (9XX numbered tags) and 7 fish (4 wild and 3 hatchery) with CH33-16 tags (3XX numbered tags). The CH32-50 tags were 32-mm in diameter, 92-mm in length, and had 87.5-g weight in air, 35.5-g weight in water with a battery life of >3-y. The CH33-16 tags are 16-mm in diameter, 87-mm in length, have 38-g weight in air, 21-g weight in water and a battery life of >1.5-y. Both tag models had external radio whip antennae that protruded through the body wall and emitted 5-s continuous bursts (10-s between each acoustic signal and 10-s between each radio signal).

Surgical implantation of transmitters in paddlefish was modified from Hart and Summerfelt (1975). Paddlefish were placed in a trough ventral side up with river water running over their gills and skin throughout the implantation procedure. Anesthesia was not used during the surgical procedure because paddlefish were released to the wild immediately upon regaining swimming ability. Surgical tools and transmitters were sterilized with ethyl alcohol before performing the surgical procedure on each paddlefish. We made a small (~15-mm) incision into the body cavity to the left of midline on the ventral surface approximately 30-mm anterior to the vent. A hypodermic needle was then externally inserted posterior to the incision to allow the radio antenna to be placed through the needle so that when the needle was removed, the antenna passed through the body (Cooke and Bunt 2001). Allowing the radio antenna to pass through the body rather than protruding through the incision provided an uncompromised piece of tissue to hold the tag thus reducing the likelihood that the incision would open if the antenna snagged (Bridger and Booth 2003). The incision was closed with five or six independent, non-

absorbable sutures. Paddlefish were then held in the river until they initiated a strong swimming response, then released near the point of capture.

Tracking was accomplished on a boat exclusively using acoustic telemetry over the study period, even though the transmitters emitted both radio and acoustic signals, because water conductivity was too high ($>700\text{-}\mu\text{S}$) for long-range radio signal detection (Winter 1996). Fish have been shown to regain normal behaviors 3-4 days post-implantation (Thoreau and Baras 1997), so we censored telemetry data acquired from tagged fish within 4-d of implantation. We attempted to search the entire 111-km study area once per week from 15 April- 15 June (paddlefish spawning period) and once per month from July-October each year of the study. No tracking occurred during the winter period due to ice and low water releases from Ft. Randall Dam. Each time a paddlefish was located, we recorded paddlefish identification number, latitude and longitude coordinates, proximity to underwater structures such as sandbars, river banks, boat ramps, or dams, in addition to habitat characteristics such as 0.2 and 0.8 depth water velocity, secchi depth, and conductivity.

Data Analysis

We used ArcGIS 9 (ESRI 2008) to plot overall movements of wild and hatchery-origin paddlefish and spring movements (e.g., spawning movements) of wild and hatchery-origin gravid female paddlefish to identify patterns. We considered 15 February-14 June the spring season using hydrology information from the relatively unaltered Niobrara River that has been found to influence paddlefish reproductive success in the study area (Pracheil et al. 2009).

We tested for difference in total distance moved between relocations between wild and hatchery origin paddlefish using a t-test. We tested for seasonal differences in average minimum distance between relocations between wild and hatchery-origin paddlefish with an analysis of variance (ANOVA) using season as a blocking factor. Season was used as a blocking factor because several studies have shown paddlefish have differential seasonal movement and habitat use (Southall and Hubert 1984; Moen et al. 1992; Zigler et al. 1999; Stancill et al. 2002; Rousch et al. 2003; Barry et al. 2007). We also tested for differences in average minimum distance between wild and hatchery origin gravid females during the spawning period using an ANOVA.

We examined randomness of segment selection by wild and hatchery-origin paddlefish using second-order habitat selection (Johnson 1980). Second-order habitat selection was determined as the aerial proportion of the home range of each fish that occurred in each segment. We then used compositional analysis (Aebischer et al. 1993), a multivariate technique that determines randomness in selection using the individual as the sampling unit through a comparison of matrices of the log-ratio of segment use to segment availability (Aebischer et al. 1993). *Post-hoc* pair-wise t-tests, without type I error correction (as in Aebischer et al. 1993), were then used to determine differences in selection between all segments. Individuals with <4 relocations total, and <2 per segment were censored from this analysis. Compositional analysis and resultant *post-hoc* tests were conducted using the “adehabitat” package (Calenge 2006) created for R software (R Development Core Team 2010).

We investigated habitat use of wild and hatchery origin paddlefish using an analysis of similarity (ANOSIM) to test for differences and two-dimensional non-metric

multidimensional scaling (NMDS) to illustrate the ANOSIM results using a Euclidean dissimilarity matrix of average seasonal habitat characteristics for each fish and also for gravid females during the spawning period. Use of the ANOSIM and NMDS techniques allowed us to assess differences in continuous habitat metrics between wild and hatchery origin paddlefish. For these analyses, we included the seasonal average of depth, water temperature, water conductivity, and flow velocity from relocations for each individual. Non-metric multidimensional scaling is an unconstrained ordination technique that, in this study, provides a visual representation of the relation of habitat use by each fish for each season. This NMDS analysis returns a graphic where the distances between each fish on the plot are directly related to the similarity of habitat use between each fish. In other words, the closer together points are on the plot, the more similar the habitat use. The NMDS analysis also returns a stress value that gives a measure of the badness of fit, in this case, in 2 dimensional space. A stress value >0.10 represents a relatively bad fit whereas a stress value of <0.10 represents a relatively good fit.

RESULTS

Paddlefish Collection and Telemetry

All paddlefish implanted with transmitters were >800 mm except for transmitter number 376—an age-3 juvenile paddlefish at the time of implantation (Table 3.1). Coded wire tag data indicated that all hatchery-origin fish were stocked in Lake Francis Case and entrained through Ft. Randall Dam, although dates when each fish was entrained are not known. Age of hatchery-origin fish, with the exception of 376, ranged from age-12 to age-15 at the time of implantation. Both wild and hatchery-origin paddlefish were relocated in all segments of the study area except for the delta (Figure

3.2, Figure 3.3, and Figure 3.4). The most common segment used by both wild (62 of 73 relocations) and hatchery (103 of 119 relocations) paddlefish was the Ft. Randall Dam tailwater segment (Figure 3.2). The riverine segment had 11 relocations (Figure 3.3) and the reservoir segment had 17 relocations (Figure 3.4).

Numbers of relocations for each paddlefish included in the study by habitat type are in Table 3.2 and were similar for wild and hatchery origin paddlefish. Average movement distances between relocations of wild and hatchery paddlefish were indiscernible. Wild paddlefish traveled an average of 13.89 ± 39.10 km between relocations whereas hatchery paddlefish traveled an average of 11.48 ± 29.13 km. There was no effect of origin (wild or hatchery) on overall distance travelled by paddlefish (t-test $t=0.44$; d.f.=20; $P=0.66$) and no effect of origin or season on average distance travelled between relocations for all paddlefish included in the study (ANOVA $F_{1,38} < 0.01$; $P=0.98$). Wild gravid female paddlefish moved an average of 0.61 ± 0.83 km between relocations during the spawning season whereas hatchery gravid female paddlefish moved an average of 0.51 ± 0.26 km between relocations during the spawning season. Wild and hatchery-origin gravid female paddlefish also showed no difference between average distances moved between relocations during the spawning season (ANOVA $F_{1,17}=0.02$; $P=0.885$). Likewise, there was no difference in abiotic factors between all wild and hatchery-origin paddlefish (ANOSIM; global-rho=-0.404; $P=0.74$) or between gravid female wild and hatchery-origin paddlefish (ANOSIM; global rho=0.056 ; $P= 0.96$). The similarities in abiotic habitat characteristics is further illustrated by the NMDS plots for all paddlefish (Figure 3.5a; stress=0.09) and gravid

female paddlefish (Figure 3.5b; stress=0.005) that do not appear to show differences between wild and hatchery-origin individuals.

Three wild and one hatchery-origin individuals were censored for the compositional analysis due to having < 4 relocations. Wild and hatchery-origin paddlefish both chose the tailwater segment over other segments (Compositional Analysis: Wild: $\Lambda = 16.696$, $df = 3$, $P < 0.001$; Hatchery: $\Lambda = 8.313$, $df = 3$, $P < 0.001$). Neither wild nor hatchery-origin paddlefish exhibited statistically detectable differences in selection of other segments.

DISCUSSION

The ability of stocked fish to behaviorally assimilate into the wild population is a key assumption to conservation and recovery plans although behaviors of wild and stocked individuals are rarely used to evaluate stocking success. The assumption that stocked fish become behaviorally integrated into the wild population appears to hold true for paddlefish movements. Movements and habitat use of hatchery and wild paddlefish appear indistinguishable after hatchery-origin paddlefish were at-large for several years (Figures 3.2- 3.5). The results of this study are similar to findings that stocked robust redhorse *Moxostoma robustum* in the Ocmulgee River, Georgia, USA exhibit similar movement patterns to those described for wild individuals (Grabowski and Jennings 2009).

Hatchery-origin gravid females also appear to behaviorally assimilate into the wild population during the spawning season (Figure 3.5b), suggesting that wild and hatchery-origin fish integrate during spawning. Furthermore, stocked paddlefish in the present study may be successfully spawning; production of young-of-year paddlefish has

been documented since the onset of stocking above and below Ft. Randall Dam (Hesse and Mestl 1993; Pracheil et al. 2009). The paddlefish population between Ft. Randall Dam and Gavins Point Dam is genetically indistinct from the paddlefish population above Ft. Randall Dam: the source population for hatchery origin individuals used in this study (Sloss et al. 2009), further lending evidence that wild and hatchery origin individuals could mix during spawning.

Hatchery-origin paddlefish had more relocations in the riverine segment than wild-origin paddlefish (Figure 3.4); although these differences were not identified in statistical tests between wild and hatchery origin paddlefish. Three of the five relocations in a slow-flowing habitat in the riverine segment were fish 376: a hatchery-origin juvenile paddlefish that was relocated near the mouth of the Niobrara River three times over one month. The habitat created by the Niobrara River confluence has been shown to be used by fishes in prior studies and is thought to provide valuable ecologic function to this area of Missouri River (Hesse and Mestl 1993; Kaemingk et al. 2007; Pracheil et al. 2009). Juvenile paddlefish have been shown to select slower flowing, non-channel habitats compared to adult paddlefish (Hoxmeier and DeVries 1997; Clark-Kolaks et al. 2009). Transmitter number 376 was the only indisputably juvenile paddlefish in the study and we were not able to collect similarly-sized wild paddlefish for telemetry purposes. The use of slow-flowing habitat is consistent with habitat use by wild juvenile paddlefish in other studies, thus suggesting that wild and hatchery origin paddlefish are also behaviorally equivalent as juveniles.

All hatchery-origin paddlefish used in this study were stocked in Lake Francis Case and entrained through Ft. Randall Dam. Entrainment of paddlefish in this system

appears to be a relatively commonplace occurrence. Approximately 50% of paddlefish in the study area are hatchery origin paddlefish stocked above Ft. Randall Dam (B. Pracheil, unpublished data) and paddlefish populations above and below Ft. Randall Dam are genetically indistinct (Sloss et al. 2009) suggesting that entrainment is integral to the population dynamics in this reach of river. There is an additional possibility that some paddlefish identified in this study as wild were also of hatchery-origin and may have biased our results: coded-wire tag retention estimates from 1992-1995 (the year classes of most of the hatchery-origin paddlefish) range from 59.7% in 1994 to 85.0% in 1992 (Mississippi Interstate Cooperative Resource Association paddlefish database, unpublished data). Movements and habitat use of wild and hatchery origin paddlefish in this study are consistent with those reported in other paddlefish movement and habitat use studies. Therefore, we do not believe that individuals identified in this study as wild but were truly hatchery-origin, that have shed a coded wire tag, biased our results.

Evaluation of behaviors of wild and hatchery fish is particularly essential if there are population-level consequences for the integration of hatchery fish into the population of wild fish. Paddlefish and related species like sturgeon that have similar life histories are being stocked with increasing frequency as part of restoration plans. Movement and characteristics of habitat use were not shown to differ in this study; however, several studies suggest that population productivity and fitness is decreased when hatchery-origin individuals integrate with wild fish. As such, behavior of paddlefish and other sturgeon species should continue to be monitored for maleffects of stocking. A population with 50% wild and 50% hatchery steelhead, for instance, was estimated to produce 63% fewer recruits-per-spawner than a population with 100% wild produced steelhead due to

reduced fecundity of hatchery steelhead (Chilcote 2003). A review of genetic studies of captive-reared animals also indicates hatchery breeding leads to selection of genes that are beneficial in captivity, but deleterious in the wild (Frankham 2008). Further studies assessing the long-term integration of hatchery-origin fish into wild fish populations are necessary to better evaluate fish species restoration programs and understand the population trajectories of long-lived, late-maturing fish.

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Table 3.1. Length, weight, sex (M—male, GF—gravid female, or U—unknown), and year class (for stocked paddlefish) by transmitter number for wild (W) and stocked (H) telemetered paddlefish.

ID #	Year Class	Length (mm)	Weight (kg)	Sex
387W		1274	32.0	GF
388W		1262	35.0	U
389W		1006	24.0	U
392W		1070	18.6	U
901W		882	10.8	U
904W		1040	15.2	U
908W		1192	31.5	GF
911W		840	7.2	U
913W		1152	22.5	GF
915W		1068	22.0	GF
376H	*	520	19.0	U
384H	1993	810	5.6	U
393H	1993	820	10.4	U
902H	1993	863	9.2	U
903H	1993 or 1994	898	9.8	U
905H	1993	916	10.4	U
906H	1995	956	10.9	U

<u>Table</u>	<u>3.1 continued</u>			
907H	1993	998	22.5	GF
909H	1996	1005	22.5	GF
910H	1995	1048	20.5	GF
912H	1993 or 1994	949	14.6	U
914H	**	939	12.4	M

Table 3.2. Implantation date, implantation location, number of relocations, total distance between relocations, and date of last relocation by transmitter number for wild (W) and hatchery (H) telemetered paddlefish.

ID #	Implantation Date	Implantation Location	# Locations	Average Distance Between Relocations \pm SD (km)	Date Last Relocation
387W	9/19/2007	Tailwater	12	0.36 \pm 0.30	8/23/2008
388W	9/5/2007	Reservoir	2	0.67	8/5/2008
389W	9/19/2007	Tailwater	3	107.96 \pm 110.00	8/23/2008
392W	9/19/2007	Tailwater	6	23.47 \pm 51.95	6/30/2008
901W	4/2/2008	Tailwater	9	1.51 \pm 2.91	8/5/2009
904W	4/2/2008	Tailwater	6	27.19 \pm 49.33	6/30/2008
908W	8/23/2007	Reservoir	1	0	8/23/2007
911W	4/2/2008	Tailwater	10	14.10 \pm 40.20	8/5/2009
913W	4/2/2008	Tailwater	13	1.85 \pm 3.52	8/5/2009
915W	4/2/2008	Tailwater	12	28.06 \pm 62.09	8/5/2009
376H	4/2/2008	Tailwater	9	7.88 \pm 21.27	8/24/2008
384H	4/2/2008	Tailwater	12	0.66 \pm 0.46	10/8/2008
393H	4/2/2008	Tailwater	8	0.47 \pm 0.32	7/1/2008
902H	4/2/2008	Tailwater	11	6.31 \pm 17.72	5/11/2009
903H	4/2/2008	Tailwater	14	23.71 \pm 56.72	8/5/2009

Table 3.2 continued

905H	4/2/2008	Tailwater	10	31.39± 65.17	8/5/2009
906H	4/2/2008	Tailwater	6	67.93± 69.64	5/21/2009
907H	9/19/2007	Tailwater	11	0.46± 0.18	8/5/2009
909H	4/2/2008	Tailwater	9	15.35± 36.06	6/9/2009
910H	4/2/2008	Tailwater	3	0.65± 0.04	4/26/2008
912H	4/2/2008	Tailwater	12	1.84± 4.00	8/5/2009
914H	4/2/2008	Tailwater	14	28.06± 62.09	8/5/2009

* Coded wire tag was not retrieved from rostrum, but likely from 2005 year class based on size.

** Information on coded wire tag was unreadable.

Table 3.3. Area (ha), number of relocations by wild or hatchery origin, and study area segment along the 111-km reach of the Missouri River between Fort Randall Dam and Gavins Point Dam.

Segment	Area (ha)	Wild Relocations	Hatchery Relocations
Tailwater	123	62	103
Riverine	4136	1	8
Delta	3693	0	0
Reservoir	11157	9	8

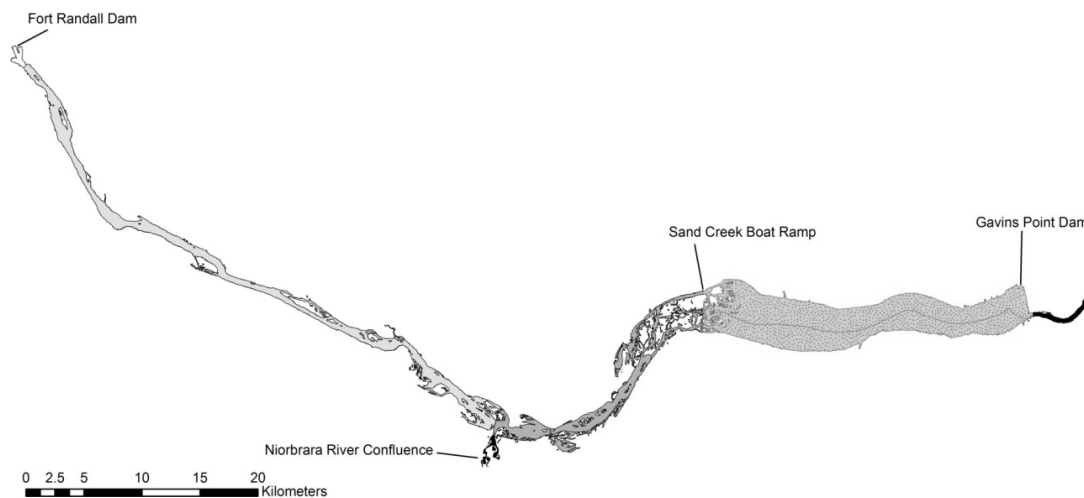


Figure 3.1. Map of Missouri River from Ft. Randall Dam to Gavins Pt. Dam denoting extent of study area and delineation of segment types. Segments were delineated as follows: Tailwater (no fill)—Ft. Randall Dam to 2-km downstream of the dam; Riverine (light gray)—2-km downstream of Ft. Randall Dam to Niobrara River Confluence; Delta (dark gray)—Niobrara River Confluence to Sand Creek Boat Ramp; Reservoir (stipple—Sand Creek Boat Ramp to Gavins Point Dam.

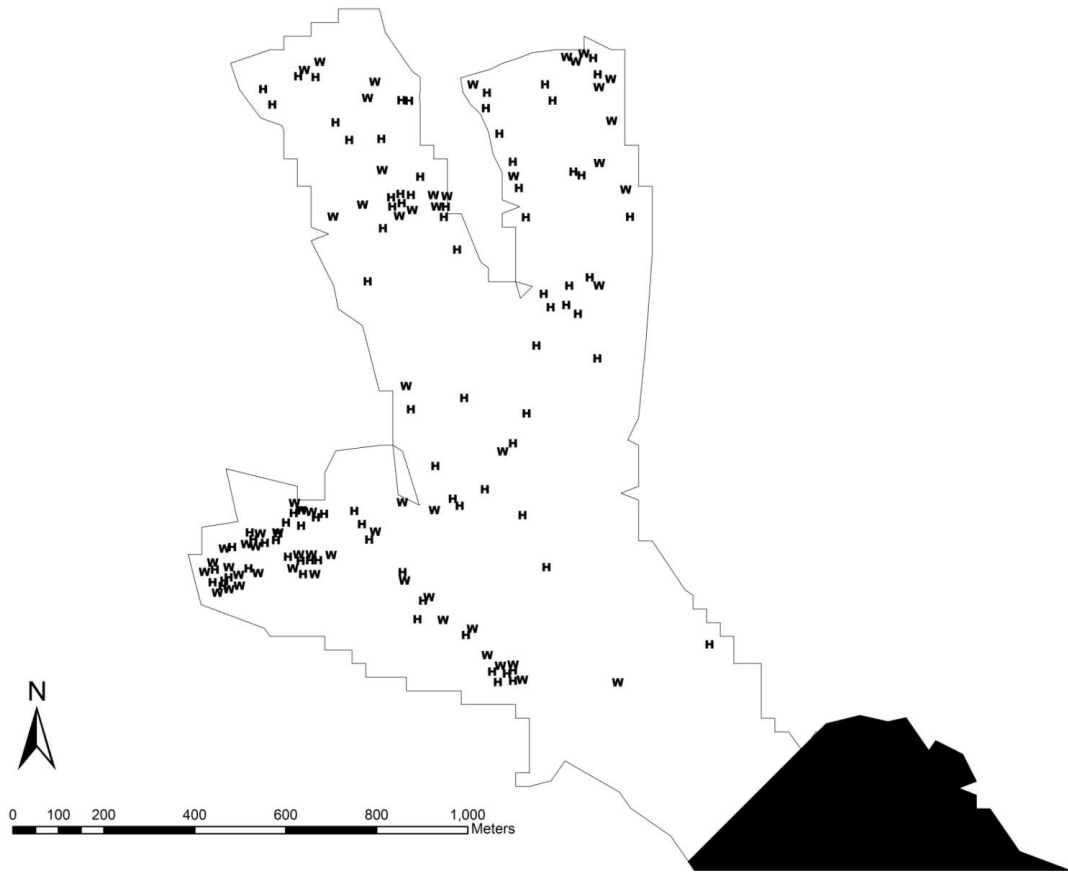


Figure 3.2. Map of Missouri River showing all relocations of wild (W) and hatchery origin (H) paddlefish in the tailwater segment.

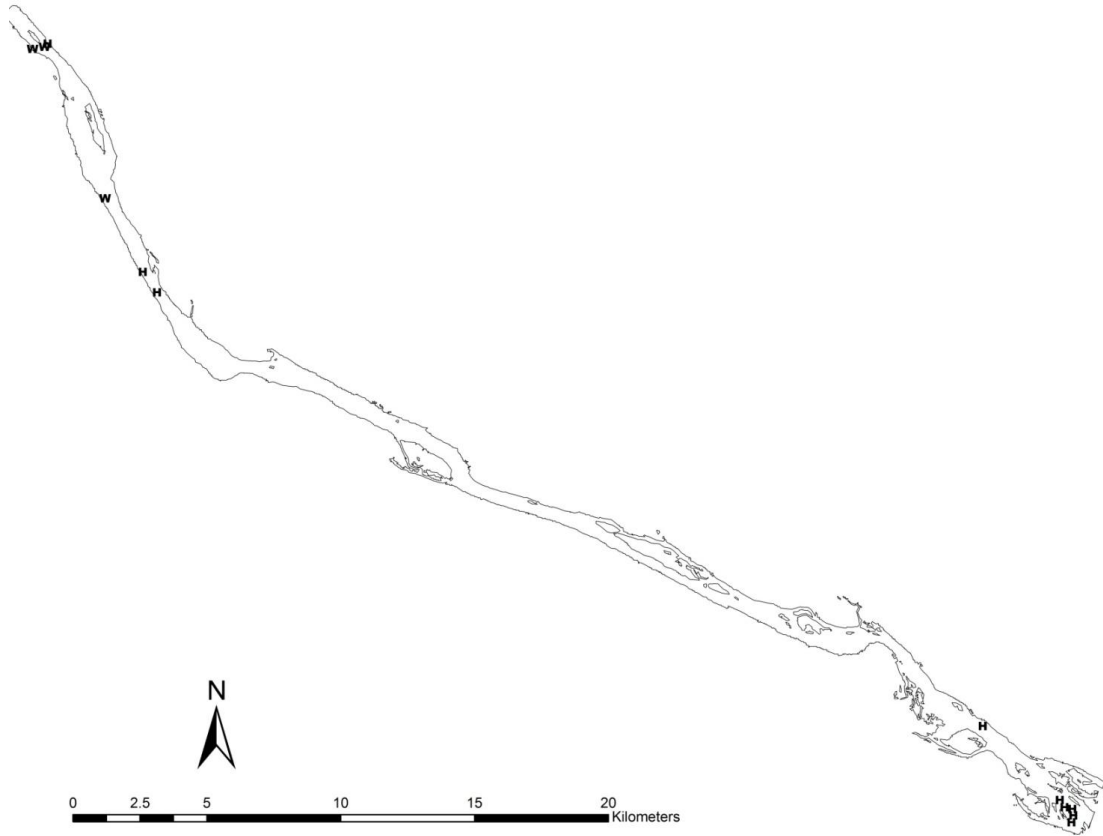


Figure 3.3. Map of Missouri River showing all relocations of wild (W) and hatchery origin (H) paddlefish in riverine segment.

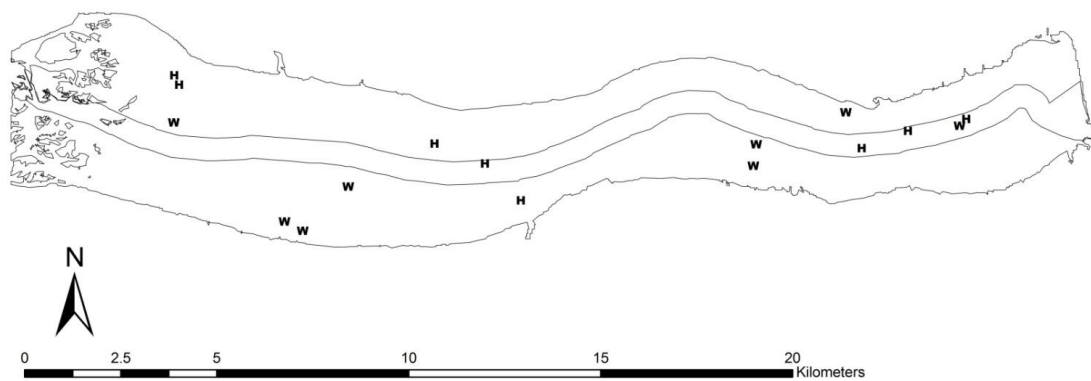


Figure 3.4. Map of Missouri River showing all relocations of wild (W) and hatchery origin (H) paddlefish in reservoir segment.

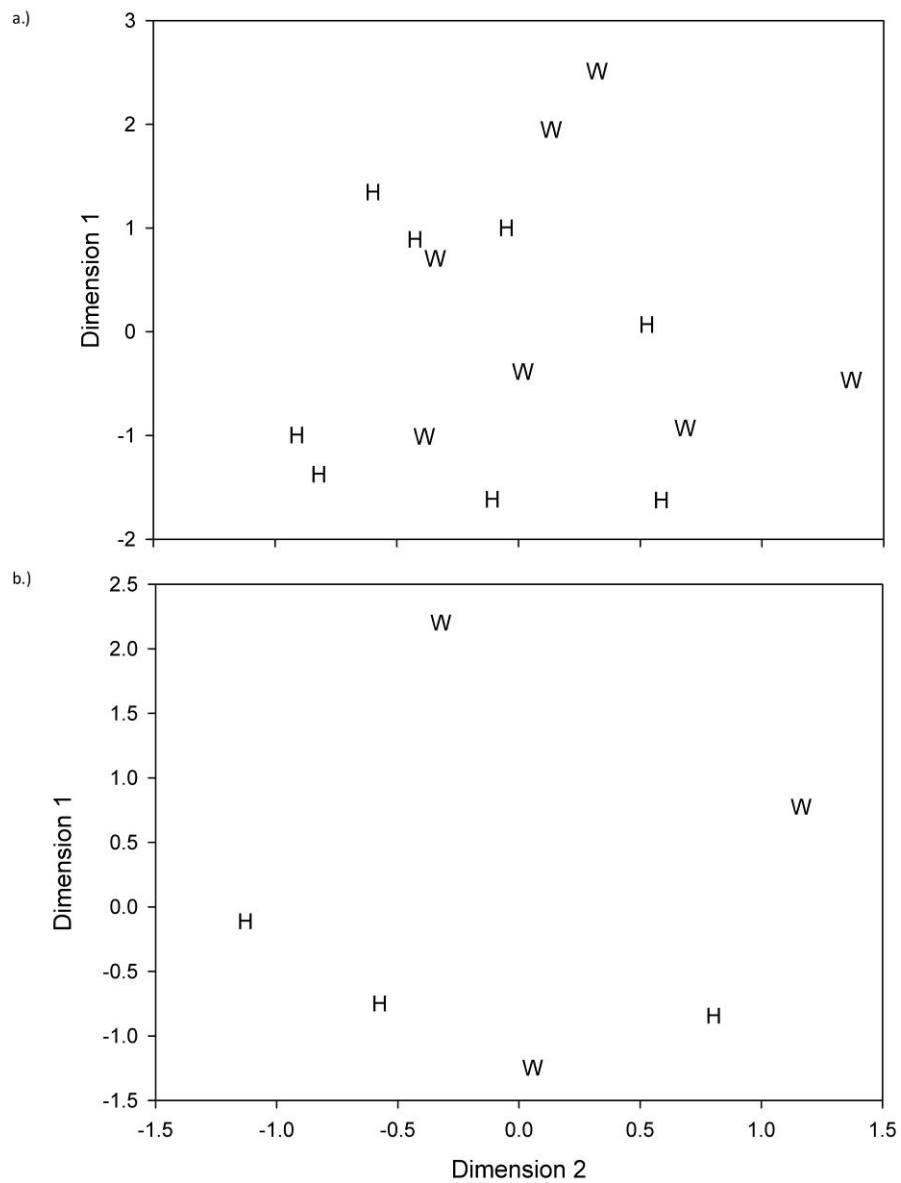


Figure 3.5. Nonmetric multidimensional scaling plot of abiotic habitat measurements (spring and summer mean flow, temperature, depth, and conductivity at relocation points) for a.) all relocated wild (W) and hatchery (H) origin paddlefish and b.) gravid wild (W) and hatchery (H) origin paddlefish.

CHAPTER 4: POPULATION CHARACTERISTICS OF THE PADDLEFISH POPULATION BETWEEN FT. RANDALL AND GAVINS POINT DAMS

ABSTRACT

The paddlefish population between Ft. Randall and Gavins Point Dam is thought to be the primary source of recruitment for the Gavins Point Dam tailwater fishery shared by Nebraska and South Dakota. Although this population is among the most extensively studied in the world and is thought to be of economic importance, an assessment of characteristics containing age and growth information has not been conducted. Additionally, stocking has not been conducted in this reach of river since 1992, but nearly half of the paddlefish population is comprised of paddlefish entrained, stocked individuals from above Ft. Randall Dam. Our study compares mortality, growth, age and length structure, and factors affecting recruitment between wild and stocked paddlefish and provides an assessment of ageing techniques used for paddlefish <20 yr. We found that length structure had not changed due to the influx of stocked paddlefish, but age structure had changed ($KS_a = 1.44$, $P = 0.03$, $n = 24$) and that year-class strength of wild paddlefish was correlated to historic young-of-year trawl data ($r^2 = 0.53$, $P = 0.02$, 11 d.f.) and year-class strength of hatchery paddlefish was correlated to numbers of paddlefish stocked above Ft. Randall Dam ($r^2 = 0.342$, $P = 0.036$, 13 d.f.). While paddlefish ageing accuracy was only 8.6% for known age paddlefish, this was similar to that reported by another study with similarly aged paddlefish. We recommend that even though this study reports no differences between wild and stocked individuals, fishery managers should

follow up on recent literature reports of differences in genetics and fitness between wild and stocked individuals in addition to continuing to tag stocked fish.

INTRODUCTION

The paddlefish population between Ft. Randall and Gavins Point dams is one of the most extensively studied paddlefish populations in the world with studies dating back to 1958 (Meyer 1960; Unkenholz 1982; Hesse and Mestl 1993; Statsny 1993; Pracheil et al. 2005; Pracheil et al. 2009). However, an assessment of the characteristics of this population containing age and growth information is conspicuously absent. This paddlefish population is thought to be one of the primary sources of recruitment to the Gavins Point Dam tailwater fishery (Hesse and Mestl 1993) — the only paddlefish fishery in the states of Nebraska and South Dakota. Young-of-year paddlefish production has been documented annually from 1965-present and was assumed to be the primary source of recruitment to the paddlefish population between Ft. Randall and Gavins Point dams (Unkenholz 1982; Hesse and Mestl 1993; Pracheil et al. 2009). Stocking has not occurred in the reach of Missouri River between the two dams since 1992, but reports of paddlefish originally stocked above Ft. Randall Dam in the Gavins Point Dam tailwater fishery by the late 1990s suggested that there were also stocked paddlefish in the reach above Gavins Point Dam. However, there was no knowledge of how or if recruitment above Gavins Point Dam was being affected by entrainment of stocked paddlefish. The potential for presence of stocked paddlefish between Ft. Randall and Gavins Point dams

created an additional need to better understand the sources of recruitment (natural versus stocking) between the two dams.

There is also a growing body of literature discussing population-level effects of stocked fish including changes in fecundity and reduced genetic diversity (see reviews by Arakai and Schmidt 2010; Laikre et al. 2010; and also Marie et al. 2010). Therefore, it is pertinent to examine the paddlefish population between Ft. Randall and Gavins Point dams to compare population characteristics between wild and stocked fish. Documented effects of stocking on paddlefish are limited, but reduced genetic diversity (Epifanio et al. 1993) and genetic differences between wild and stocked paddlefish (Sloss et al. 2009) have been reported.

Data are available for the paddlefish population between Ft. Randall and Gavins Point dams that provide for a retrospective examination of population characteristics in context with current findings. Moreover, focused data collection efforts before large amounts of stocking were conducted above Ft. Randall Dam allow for the comparison of characteristics before and after entrained, stocked paddlefish became a substantial constituent of the population. This study aimed to describe the population characteristics including age structure, length structure, growth, and factors associated with recruitment of wild and stocked paddlefish between Ft. Randall Dam and Gavins Point Dam on the Missouri River as well as provide management recommendations for paddlefish fishery managers throughout their range.

STUDY AREA

The study area was the portion of the Missouri River in South Dakota and Nebraska extending from Big Bend Dam downstream to the Gavins Point Dam tailwater (Figure 4.1). Lake Francis Case is a 172 km long, 41,000 ha reservoir formed by Ft. Randall Dam, the third smallest dam on the mainstem Missouri River. No riverine reach exists between Ft. Randall Dam and the next upstream dam, Big Bend Dam. Average annual discharge at Ft. Randall Dam was $699 \text{ m}^3 \cdot \text{s}^{-1}$ between 1965-2007 (Pracheil et al. 2009). Natural paddlefish recruitment in Lake Francis Case is considered absent or negligible (Pierce 2010). The reach of Missouri River between Ft. Randall and Gavins Point dams contains both river and reservoir reaches—a 71 km unchannelized riverine reach extending from Ft. Randall Dam to just below the confluence of the Niobrara and Missouri rivers, and a 40 km long reservoir, Lewis and Clark Lake. Lewis and Clark Lake is formed by Gavins Point Dam, the smallest and downstream-most dam on the mainstem Missouri River with a mean annual discharge of $914 \text{ m}^3 \cdot \text{s}^{-1}$ between 1965-2007 (Pracheil et al. 2009). In addition to natural recruitment annually from 1965-present (Unkenholz 1982; Hesse and Mestl 1993; Pracheil et al. 2009), paddlefish were also stocked between Fort Randall and Gavins Point dams from 1988-1992 and in Lake Francis Case nearly annually from 1990-present.

MATERIALS AND METHODS

Our analyses relied on several key pieces of information combined from multiple data sources to understand population characteristics through time including age structure, mortality, length distributions, recruitment, and stocking records in our study

area. Our approach allowed us to capitalize on long-term data collection efforts in the study area that better enabled us to evaluate trends.

Data sources

Extensive paddlefish data collection has occurred in the study area since 1958 and many of these data were incorporated into our analyses. We used young-of-year (yoy) paddlefish trawl catch per unit effort (CPUE) data collected in Lewis and Clark Lake annually from 1965 to 2007. Methods for the yoy paddlefish trawl are detailed in Hesse and Mestl (1993). We obtained paddlefish stocking histories for Lake Francis Case and Lewis and Clark Lake from the Mississippi Interstate Cooperative Resource Association (MICRA) paddlefish stock assessment database that contains numbers of paddlefish stocked each year in Lake Francis Case and Lewis and Clark Lake from 1990 to present. Historic paddlefish length-frequency data were taken from 1990-1991 (Statsny 1992). Detailed collection methods are described in Statsny (1992), but they are similar to methods listed under *Current paddlefish collection*.

Current paddlefish collection

We collected paddlefish data throughout the study reach during the months of April-October 2007-2009 using 61 m long by 3 m high floating trammel nets with 750 mm outer mesh and 80 mm inner mesh; 183 m long by 3 m high fixed-position floating gill nets with 80 mm mesh; and 274 m long (hobbled to 183 m long) by 4 m high fixed-position floating gill nets with 80 mm mesh. Although the entire reach between Ft. Randall and Gavins Point dams was sampled for paddlefish, effort was concentrated on the Ft. Randall Dam tailwater because paddlefish were highly concentrated in that area.

A concurrent telemetry study (Chapter 3) also indicated that paddlefish in this reach of Missouri River move throughout the study area, thus we assumed paddlefish sampled in the Ft. Randall tailwater were representative of the population at-large. We checked paddlefish for coded-wire tags (CWT) with a CWT detection wand (Northwest Marine Technologies, Shaw Island, WA). When CWTs were detected, a small piece of paddlefish rostrum containing the CWT was removed and sent to the United States Fish and Wildlife Service Fisheries Resource Office in Columbia, MO for tag reading and inclusion in the MICRA Paddlefish Stock Assessment Database. Paddlefish identified as hatchery-origin were indisputably of hatchery-origin because their coded-wire tag linked them to a stocking location and date; however, because tag loss through natural processes or through losing the part of the rostrum containing the CWT can occur, it is possible that some paddlefish without coded-wire tags are of hatchery-origin. However, paddlefish where CWTs were not detected are further described as being of wild-origin, although we do acknowledge that some of the individuals identified as wild may be hatchery-origin individuals that have shed their CWTs. Weights and eye-to-fork length (length from front of eye to fork of tail; Ruelle and Hudson 1977) of all paddlefish were recorded.

Age and growth analysis

We conducted age and growth analyses from jawbones of 46 wild paddlefish and 37 hatchery-origin paddlefish (Adams 1942; Scarnecchia et al. 2006) collected between June and September, 2009. Age was determined from paddlefish jawbones that were mounted in epoxy resin and then cut with an isomet-low speed saw to 0.8 mm thickness before being mounted on glass slides. Digital photographs of sectioned jawbones were

taken and aged independently by two readers. Annuli can become difficult to distinguish in long-lived fish such as paddlefish so we included tolerance limits for between reader disagreements following Scarnecchia et al. (2006). Ages for each fish were assigned by the primary reader when reader agreement was ± 1 year for fish < age 20, ± 2 years for fish age 20-34, and ± 3 years for fish > age 35. Ages of jaws that did not fall within these tolerance limits were mutually agreed upon by the primary and secondary reader. We used jaw bones from 12 hatchery-origin paddlefish of known age to assess our ageing technique. We additionally used ages retrieved from the CWTs of the 219 hatchery-origin paddlefish (including the 12 hatchery-origin paddlefish with ages read from jaws). We estimated back-calculated lengths at age from dentary annuli using Fish BC software (Doll and Lauer 2007). Additionally, we fit von Bertalanffy growth curves according to methods by Isely and Grabowski (2007) to describe growth of wild and hatchery-origin paddlefish using jaw bone derived ages for wild fish and CWT derived ages from all hatchery-origin paddlefish. We tested for differences between von Bertalanffy growth curves of wild and stocked paddlefish by comparing 95% confidence intervals of parameter estimates for wild and stocked paddlefish and all paddlefish irrespective of origin.

We used Kolmogorov-Smirnov tests to determine if there were differences between age frequency distributions for wild and hatchery-origin paddlefish in the 2007-2009 study, between length-frequency distributions of paddlefish >400 mm from the 1990-1991 population and the 2007-2009 population, and between wild and hatchery-origin paddlefish in the 2007-2009 population. We assessed factors influencing

recruitment of wild and hatchery origin paddlefish using a Pearson's correlation. We assessed factors affecting wild fish recruitment by correlating yoy trawl CPUE from the year wild fish were determined to have been produced with the number of wild fish collected from a year-class. We assessed factors influencing hatchery fish recruitment by correlating the number of fish stocked in Lake Francis Case in a year-class with the number of paddlefish recaptured from a year-class.

We also used age information to conduct catch-curve regression analyses to determine mortality for the overall population for wild and hatchery-origin paddlefish separately to determine if there were any differences in apparent mortality between wild and stocked paddlefish. Wild paddlefish catch-curve regressions were used to represent the overall population mortality because their year-class strength was presumably not influenced by numbers of paddlefish stocked. We tested for differences in mortality between wild and stocked paddlefish by using an analysis of covariance (ANCOVA) to test for significant differences in slopes of the catch-curve regression including all ages of paddlefish. We tested for differences in mortality of wild and hatchery-origin paddlefish using an ANCOVA to compare slopes of catch-curve regression analyses with paddlefish of comparable age (ages 12-18).

RESULTS

A total of 477 individual paddlefish were sampled between Ft. Randall and Gavins Point dams between 2007 and 2009. Stocked paddlefish entrained through Ft. Randall Dam accounted for 31% of 113 paddlefish sampled in 2007, 48% of 109 paddlefish sampled in 2008, and 38% of 255 paddlefish sampled in 2009. Only four

paddlefish sampled were originally stocked between Ft. Randall and Gavins Point dams from 1988-1992 accounting for <1% of paddlefish sampled and <2% of stocked paddlefish sampled.

Age and growth analysis

Length distributions of paddlefish >400 mm did not differ between the 1991-1992 study and 2007-2009 study ($KS_a = 0.463$, $P = 0.983$; Figure 4.2). Likewise, length distributions of wild and hatchery-origin paddlefish from the 2007-2009 study did not differ. However, the distribution of ages of wild and hatchery-origin paddlefish differed ($KS_a = 1.44$, $P = 0.03$, $n = 24$; Figure 4.3); wild paddlefish contained individuals from older year-classes than the hatchery-origin paddlefish.

Our final age estimates using dentaries differed from known-age individuals by an average of 2.37 yr. Reader 1 determined the correct age for one out of 12 fish and deviated from actual age by an average of 2.37 yr; whereas reader 2 determined the correct age for zero out of 12 fish and deviated from actual age by an average of 2.47 yr (Figure 4.4). When the tolerance for minor disagreement (Scarnecchia et al. 2006) was employed for known age fish, reader 1 assigned the correct age to three out of 12 fish and reader 2 assigned the correct age to two out of 12 fish.

There were no differences in mean back-calculated lengths-at-age between wild and hatchery-origin paddlefish; standard errors of all back-calculated lengths-at-age overlapped (Table 1; Figure 4.5). There were no differences between 95% confidence intervals of Von Bertalanffy growth curve parameter estimates for wild and stocked

paddlefish and no difference between parameter estimates for wild, stocked, or pooled parameter estimates (Table 4.2; Figure 4.6).

Catch-curve regressions indicated that instantaneous mortality of the population was 0.78 ± 0.12 and annual mortality was $54.2 \pm 5.1\%$. Catch-curve regressions calculated with wild and stocked paddlefish did not have different slopes (wild: $y=12.51x-0.78$; stocked: $y=14.84x-0.83$; difference between slopes: $F_{1,47}=3.70$; $P=0.0605$). Similarly, when comparing slopes of catch-curve regressions between wild and stocked paddlefish of similar ages (ages 12-18), mortality rates were not significantly different (wild: $y=.014x+3.10$; stocked: $y=0.29x-1.67$; difference between slopes: $F_{1,47}=0.55$; $P=0.47$).

Correlates of recruitment for wild and stocked paddlefish differed. Frequencies of hatchery-origin paddlefish in a year-class were not correlated with long-term yoy paddlefish trawl data ($r=0.349$, $P=0.24$, 13 d.f.), but were correlated with stocking of paddlefish in Lake Francis Case (Figure 4.6 a; $r=0.53$, $P=0.02$, 15 d.f.). Removing the outlier (108 recaptures, 44,709 stocked) in the correlation between numbers of paddlefish stocked in Lake Francis Case and the number of paddlefish collected from a year-class between Ft. Randall and Gavins Point dams yields a positive relationship ($r=0.516$, $P=0.059$, 14 d.f.). Frequencies of wild paddlefish in a year-class were not correlated with numbers of paddlefish stocked in a year-class in Lake Francis Case ($r=-0.007$, $P=0.981$, 17 d.f.), but were correlated with long-term young-of-year (yoy) paddlefish trawl data from the same year-class (Figure 4.6 b; $r=0.586$, $P=0.013$, 17 d.f.).

DISCUSSION

Entrainment of stocked paddlefish in this reach of the Missouri River has resulted in large numbers of stocked paddlefish downstream of Ft. Randall Dam. Accumulation of younger, stocked paddlefish between Ft. Randall and Gavins Point dams has influenced the age structure causing a change in demographic structure that may need to factor into management decisions, particularly for the Gavins Point Dam tailwater fishery. However, other population metrics, such as mortality and growth, do not appear to be affected.

Ages derived from reading jawbones of paddlefish <20 yr were only accurate 8.3% of the time (% correct from reader 1), but our rates for correctly assigning age based on dentaries are similar to those reported in other studies of known-age paddlefish. For example, Pierce (2010) reported 8.6% accuracy of determining true age of known-age fish in Lake Francis Case. It is clear, from the results of the present study and Pierce (2010) that the science of determining paddlefish age by counting dentary annuli requires some refinement to provide accurate estimates of age to researchers. The population of paddlefish between Ft. Randall and Gavins Point dam, to this end, can provide a unique opportunity to advance techniques used in paddlefish ageing because of the very large proportion of known age paddlefish.

Mortality of wild paddlefish in this population is higher than in Lake Francis Case. For example, instantaneous (0.78 ± 0.12) and annual mortality ($54.2 \pm 5.1\%$). in the Ft. Randall to Gavins Point dam reach of the Missouri River are greater than instantaneous (0.16 ± 0.05) and annual ($14.4 \pm 4.7\%$) mortality reported above Ft. Randall Dam in Lake Francis Case. Higher mortality rates below Ft. Randall Dam could be an

artifact of potentially larger proportions of the population being entrained through Gavins Point Dam than is entrained through Ft. Randall Dam. High proportions of the population between Ft. Randall and Gavins Point dams are entrained. For example, only four of the 102,650 paddlefish originally stocked in Lewis and Clark Lake from 1988-1992 were recaptured during our sampling in 2007-2009. Comparatively, 57 paddlefish stocked in Lewis and Clark Lake were recaptured below Gavins Point Dam from 2007-2009 and 595 were recaptured below Gavins Point Dam from 1995-2009 (MICRA, unpublished data). A greater proportion of the population may be vulnerable to entrainment below Ft. Randall Dam because Lewis and Clark Lake is not as large as Lake Francis Case, yet has greater annual water releases (Pracheil et al. 2009).

Maximum size of paddlefish in this reach of Missouri River was approximately 200 mm smaller than that in Lake Francis Case ($L_{\infty}=1,325$; Pierce 2010). This difference in maximum length between the Lake Francis Case and current study populations may be attributed to the greater availability of reservoir habitat above Ft. Randall Dam. Paukert and Fisher (2001) found that paddlefish in reservoirs, such as Lake Francis Case, are larger than paddlefish in riverine reaches presumably due to greater food availability and lower energetic requirements. Alternatively, comparatively harsh environmental conditions below Ft. Randall Dam brought about by hydrologic alterations may also be increasing mortality rates and attributing to the lower L_{∞} compared to paddlefish in Lake Francis Case. For instance, paddlefish frequently select tailwater habitat below Ft. Randall Dam that contains cold, hypolimnetic water releases (Chapter 3). Similar

hypolimnetic releases have been reported to reduce fish growth on the Colorado River (Clarkson and Childs 2000).

Entrainment of stocked paddlefish can change drivers of recruitment and year-class strength (Figure 4.6). Year-class strength of stocked paddlefish is influenced by the numbers of paddlefish stocked in Lake Francis Case—the more paddlefish of a given year-class that are stocked in Lake Francis Case, the more paddlefish become entrained through Ft. Randall Dam (Figure 4.6 a). Year-class strength of wild paddlefish, on the other hand, is related to the number of young-of-year paddlefish produced in a year (Figure 4.6 b) and hence, would be influenced by the same factors that affect natural young-of-year paddlefish recruitment. Natural paddlefish recruitment between Ft. Randall and Gavins Point dams has been shown to be influenced by flows from the relatively unregulated Niobrara River (Pracheil et al. 2009)—a tributary that joins the Missouri River between Ft. Randall and Gavins Point dams (Figure 4.1). Year-class strength is often used to inform and evaluate management actions like harvest regulations (Maceina and Pereira 2007). Understanding the dichotomous nature of recruitment in this system may be useful for making future management decisions. For instance, this paddlefish population is suspected to be a primary source of paddlefish recruitment for the Gavins Point Dam tailwater fishery, and gaining a more complete understanding of recruitment dynamics may be useful in setting sustainable harvest regulations.

Management Recommendations

This study did not find wild and stocked paddlefish to have differences in growth or mortality, but extra care must still be taken when making decisions of how, when,

where, or if, to stock. Planning steps prior to stocking paddlefish, such as marking stocked fish, are critical for understanding how hatchery-origin individuals are incorporated into a population—a process that takes many years to observe because of long life-spans and times to maturity. Comparing characteristics of wild and stocked paddlefish or knowing that there were stocked paddlefish moving through dams, for instance, would not be possible if stocked paddlefish were not marked with CWTs. Further studies also need to assess whether hatchery-origin and wild paddlefish are successfully breeding and if so, if the offspring are genetically domesticated compared to the wild fish. A recent study reports hatchery-origin individuals in this study area display genetic evidence of domestication selection (selection of genes beneficial to life in a hatchery; Sloss et al. 2009) that can lead to genetic introgression if the wild and hatchery-origin fish interbreed. Further studies examining if these genotypic differences between wild and stocked fish have phenotypic correlates, such as differences in life-span, fecundity, or other factors that could impact fitness, would aid in understanding the role of stocking in population dynamics. Additionally, several studies have shown individual fish to delay maturity (Spangler et al. 1977; Scheuller et al. 2005) or reduce fecundity with increasing population density (Bowen et al. 1991). The large influx of stocked paddlefish in this reach of river could be having similar density-dependent effects on the population; however, further studies will be necessary to determine if density dependence is impacting either fecundity or age at maturity.

Entrainment appears to be an important driver for paddlefish population dynamics in this reach of Missouri River, but it may also be an important driver of population

dynamics at a larger scale. It is unclear whether the population between Ft. Randall and Gavins Point dams is viable without subsidies of entrained, stocked paddlefish.

Furthermore, the numeric contribution of paddlefish entrained through Gavins Point Dam to downstream populations is unknown, but suspected to be important. Ending or altering stocking rates in Lake Francis Case, may lead to population declines downstream of Gavins Point Dam if downstream populations also rely on subsidies of stocked paddlefish from Lake Francis Case. Future studies that quantify the extent the Lewis and Clark Lake population influences downstream populations are critical to developing a greater understanding of how stocking rates in Lake Francis Case are influencing populations further downstream.

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Table 4.1. Mean back-calculated length-at-age \pm standard deviation (N) for wild and hatchery-origin paddlefish, and all paddlefish irrespective of origin (combined) from the Missouri River between Ft. Randall and Gavins Point dams.

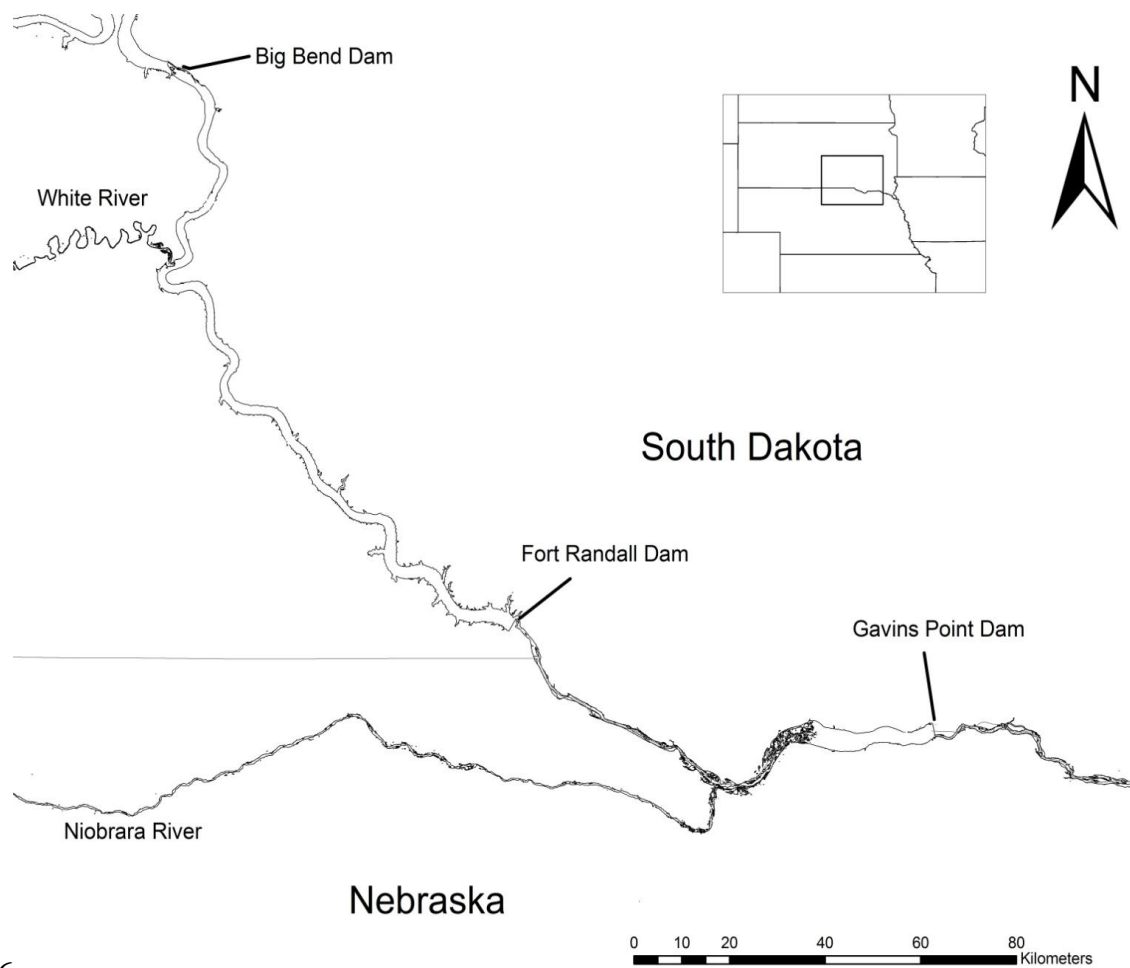
Age	Wild	Hatchery	Combined
1	156.4 \pm 11.3 (46)	163.3 \pm 7.8 (37)	157.3 \pm 7.0 (83)
2	270.4 \pm 13.7 (46)	274.4 \pm 8.7 (37)	267.6 \pm 8.7 (83)
3	363.7 \pm 15.3 (46)	367.2 \pm 9.9 (37)	358.7 \pm 10.2 (83)
4	451.9 \pm 18.0 (46)	449.8 \pm 11.6 (37)	442.8 \pm 12.1 (83)
5	527.7 \pm 19.6 (45)	516.2 \pm 12.1 (36)	512.7 \pm 13.5 (81)
6	592.0 \pm 20.0 (44)	575.1 \pm 13.5 (36)	573.0 \pm 14.4 (80)
7	645.1 \pm 19.1 (43)	625.7 \pm 13.5 (36)	623.4 \pm 14.6 (79)
8	690.1 \pm 19.7 (41)	678.2 \pm 14.2 (36)	670.3 \pm 15.5 (77)
9	731.5 \pm 20.3 (40)	722.2 \pm 14.8 (35)	711.5 \pm 16.4 (75)
10	768.6 \pm 21.4 (38)	760.5 \pm 14.5 (35)	747.7 \pm 17.2 (73)
11	787.8 \pm 20.9 (35)	788.0 \pm 15.6 (31)	768.4 \pm 18.5 (66)
12	820.4 \pm 22.8 (29)	816.5 \pm 17.1 (28)	795.1 \pm 21.1 (57)
13	837.1 \pm 24.3 (26)	845.3 \pm 16.7 (28)	816.0 \pm 22.3 (54)
14	848.9 \pm 24.1 (23)	861.7 \pm 19.4 (22)	824.5 \pm 25.7 (55)
15	852.0 \pm 27.4 (18)	893.2 \pm 21.6 (19)	835.7 \pm 30.5 (37)
16	879.6 \pm 28.8 (17)	916.2 \pm 27.6 (14)	851.4 \pm 35.9 (31)
17	905.7 \pm 32.3 (15)	895.3 \pm 29.8 (8)	842.9 \pm 45.4 (23)
18	917.6 \pm 39.5 (12)		879.3 \pm 52.0 (16)

Table 4.1 continued.

19	915.5 ± 41.2 (9)	843.1 ± 72.4 (10)
20	932.1 ± 45.7 (7)	923.3 ± 40.5 (8)
21	156.4 ± 36.7 (6)	920.8 ± 36.7 (6)
22	270.4 ± 36.5 (6)	939.6 ± 36.5 (6)
23	363.7 ± 42.1 (5)	970.6 ± 42.1 (5)

Table 4.2. Estimates of L_{∞} , k_0 , and t_0 (95% confidence estimates) for Von Bertalanffy growth functions for wild and stocked paddlefish.

	Wild	Stocked	Combined
L_{∞}	1090.4	1071.0	1131.0
	(984.3-1196.4)	(823.5-1318.4)	(965.9-1296.1)
k	0.102	0.086	0.074
	(0.017-0.187)	(0.002-0.170)	(0.013-0.135)
t_0	-8.065	-4.971	-11.292
	(-17.883-1.753)	(-12.653-2.712)	(-21.554- -1.029)



.6

Figure 4.1. Map of study area on the Missouri River from Big Bend Dam near Chamberlain, SD to the tailwater of Gavins Point Dam near Yankton, SD. Gavins Point Dam forms the reservoir Lewis and Clark Lake and Ft. Randall Dam forms the reservoir Lake Francis Case.

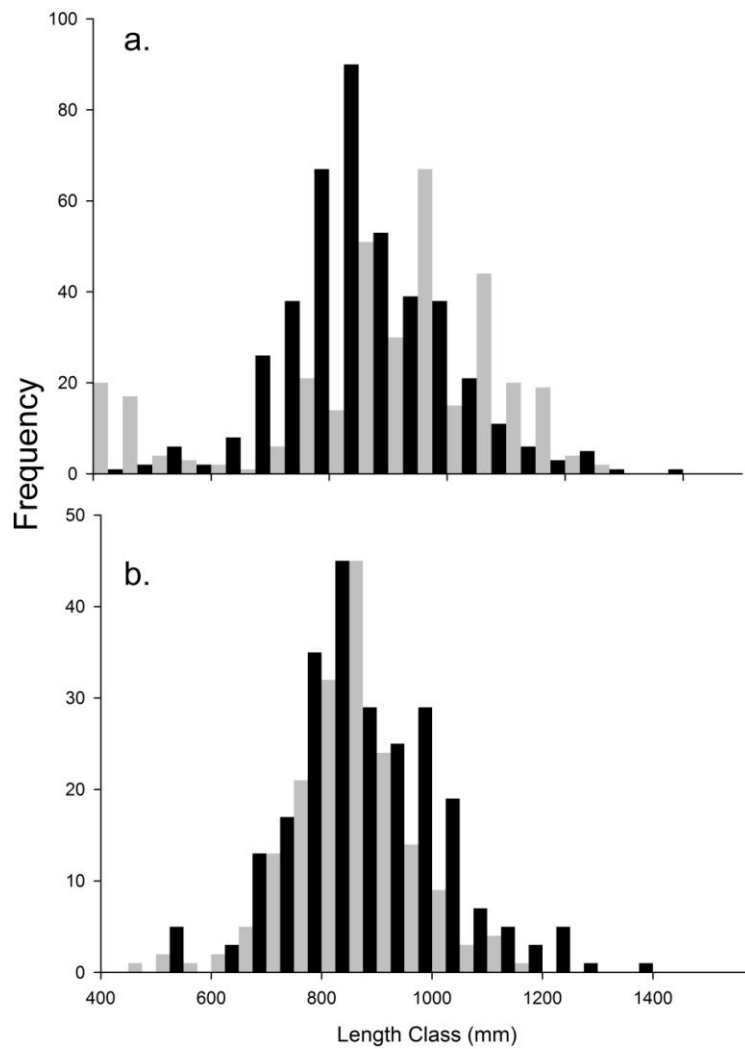


Figure 4.2. Length-frequency distributions for a.) the 1991-1992 paddlefish population (gray bars; Statsny 1993) and the 2007-2009 paddlefish population (black bars) and b.) wild (black bars) and hatchery-origin (gray bars) paddlefish collected between Ft. Randall Dam and Gavins Point Dam on the Missouri River from 2007-2009.

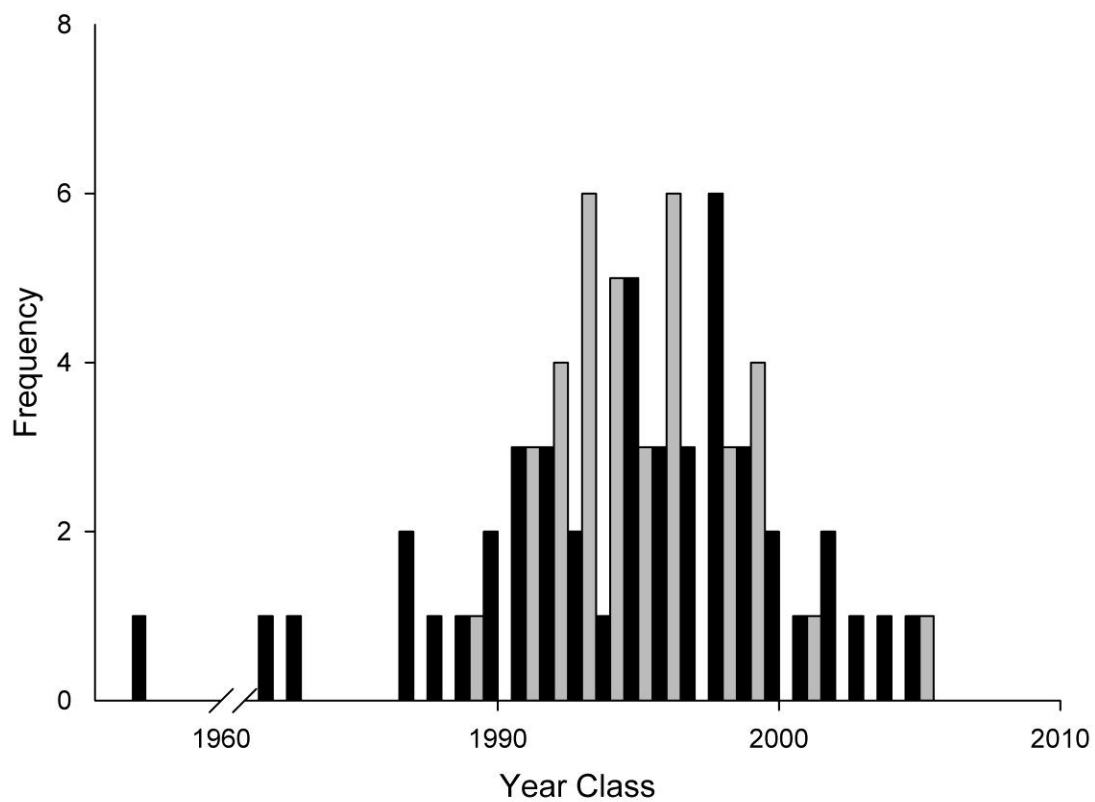


Figure 4.3. Year-class frequency distribution of wild (black bars) and hatchery-origin (gray bars) paddlefish collected between Ft. Randall Dam and Gavins Point Dam on the Missouri River in 2009.

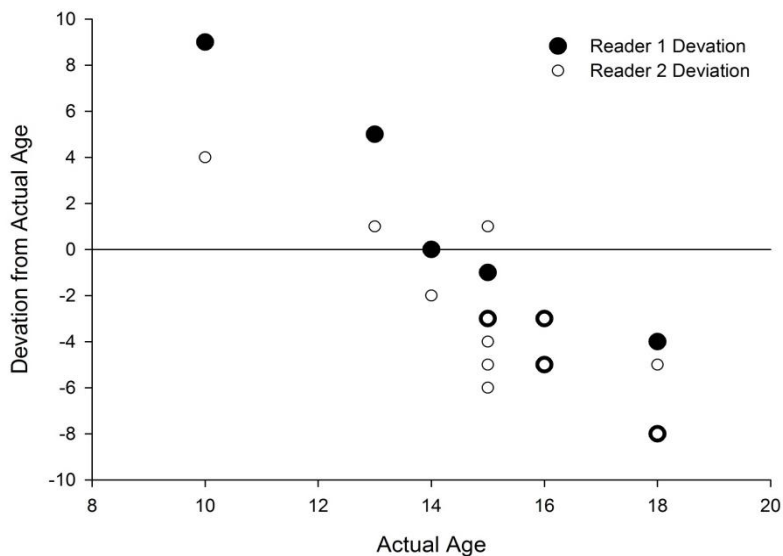


Figure 4.4. Discrepancies between paddlefish age as for 15 paddlefish as determined by two readers (reader 1, solid black dots; reader 2, hollow dots) and actual age as determined by known age hatchery-reared paddlefish. Discrepancies are depicted as deviations of reader determined years (plus or minus years on y-axis—no deviation is represented by 0-line on y-axis) from the known age (x-axis). Points representing reader 1 deviation are larger so they can be seen behind points representing reader 2.

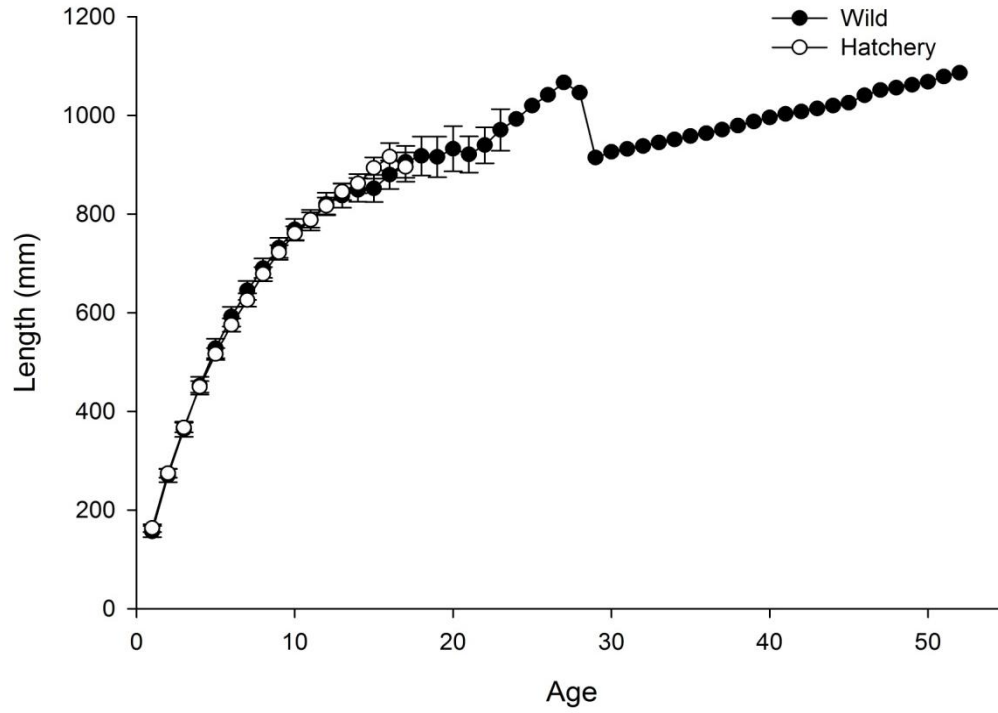


Figure 4.5 Mean back-calculated length-at-age \pm standard error for wild (black circles) and hatchery paddlefish between Ft. Randall and Gavins Point dams.

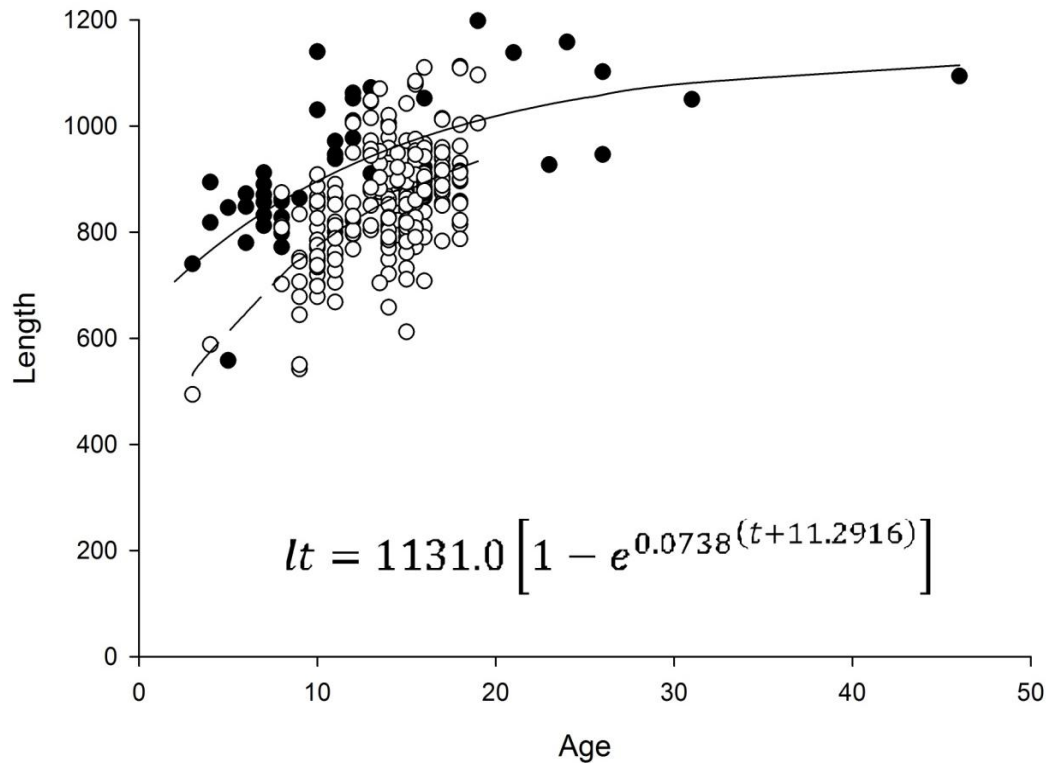


Figure 4.6. Age-length scatterplot for wild (N=42; hollow dots) and hatchery-origin (N=204; black dots) paddlefish collected between Ft. Randall Dam and Gavins Point Dam on the Missouri River from 2007-2009 using reader determined age for wild paddlefish and coded wire tag age from hatchery paddlefish. Equation for Von Bertalanffy growth function with wild and hatchery origin paddlefish combined is shown on the graph. The solid line on the graph represents the Von Bertalanffy growth function for the pooled wild and stocked paddlefish and the dashed line represents the Von Bertalanffy growth function for known-age hatchery-reared paddlefish.

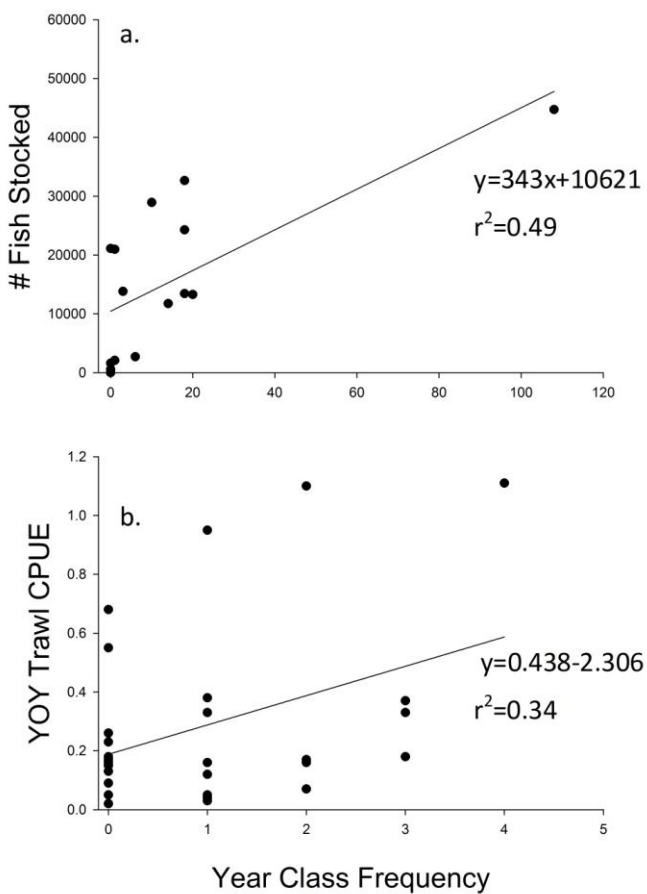


Figure 4.7. Year-class frequency and a.) number of paddlefis stocked in Lake Francis Case per year from 1990-2009 and b.) young-of-year paddlefis trawl data by year from 1965-2009. Lines in both graphs are best fit linear regression lines. Equations for best-fit linear regression lines are shown on the graphs.

CHAPTER 5: MOVEMENT AND SURVIVAL OF WILD AND STOCKED PADDLEFISH ACROSS THEIR SPECIES RANGE: IMPLICATIONS FOR MANAGEMENT OF MIGRATORY FISHES

ABSTRACT

Migratory freshwater fish have sustained substantial declines globally due to factors such as habitat loss and overharvest. Attempts at large-scale conservation plans for these fishes have been made in the USA through the Mississippi River Interstate Cooperative Resource Association (MICRA) paddlefish and sturgeon committee, established in 1993, to mitigate for the current state-specific management of paddlefish and sturgeon, thus, regulations and conservation status of Acipenserids are determined by individual states. The results of the MICRA effort have been a long-term, nearly range-wide mark-recapture database containing information on >30,000 individually marked wild paddlefish and >2 million batch marked hatchery-reared paddlefish. We used data from the paddlefish stock assessment database to describe 1.) survival and recapture probabilities of paddlefish, 2.) the spatial extent of wild and stocked paddlefish movements and 3.) concomitant management implications of these survival and movements estimates. Annual survival probability estimates of wild paddlefish were lowest for the Mississippi River Basin (0.64) and highest for the Missouri River Basin (0.87). Survival, recapture and movement probability estimates for stocked paddlefish were not reliable (very wide or suspiciously small confidence estimates) likely due to a very small number of recaptures compared to the number of stocked fish at large (recaptures <1%). Movement into and out of river basins suggests that current migratory

fish management conducted on a state-specific basis may not be of a sufficient spatial-scale to effectively manage migratory fish populations.

INTRODUCTION

Impoundment of rivers has blocked spawning migrations and has been a prime source of habitat loss leading to declines in freshwater migratory fishes (Allen and Flecker 1993; Dudgeon 2006). For example, the Order Acipenseriformes (paddlefish and sturgeons), an Order containing many migratory freshwater fish species, has been named the most critically endangered taxa on earth by the 2010 International Union of Conservation of Nature (IUCN). The precarious state of freshwater migratory fishes places natural resource managers and policy makers at a critical crossroads in creating species recovery plans and fulfilling management objectives that range from species conservation to commercial and sport harvest.

A potential intensifying factor in the decline of migratory fishes in the USA is state-specific management that may not be implemented at a sufficient spatial scale to incorporate large-scale movements of migratory fishes. For example, blue suckers *Cycoreon elongatus* are capable of migrations spanning >200 km and multiple river systems annually (Neely et al. 2009). Additionally, recruitment of shovelnose sturgeon *Scaphirhynchus platyrhynchus* and federally endangered pallid sturgeon *S. albus* require hundreds of km of unimpeded larval drift distance (Braaten et al. 2008) typically carrying larvae across one or more state lines.

Attempts have been made to implement large-scale conservation measures for migratory fishes in the USA, particularly for fishes of the Order Acipenseriformes. For example, the Mississippi River Interstate Cooperative Resource Association (MICRA) paddlefish and sturgeon committee was formed in 1993 to provide cohesive sampling, management, and conservation of Acipenserid fishes of the Mississippi River basin among its member states. The MICRA consists of voluntary cooperation among member states from within the basin, the United States Fish and Wildlife Service, Tennessee Valley Authority, U.S. Bureau of Reclamation, U.S. Geological Survey, Chickasaw Indian Nation, and the Chippewa-Cree Indian Tribe. The MICRA paddlefish and sturgeon committee created a nationwide paddlefish stock assessment (hereafter, MICRA database) in 1995 by undertaking a range-wide, mark-recapture study (with the exception of the state of Montana) along with an accompanying database that also contains hatchery release and recapture information since 1990.

The MICRA database provides a unique opportunity to examine a migratory fish at a nearly range-wide scale and specifically has the potential to provide large-scale estimates of survival and movement for a migratory fish. We thus used the MICRA paddlefish stock assessment database as a general case for understanding migratory freshwater fish at a very large spatial scale. Our specific objectives were to describe 1.) survival and recapture probabilities of paddlefish, 2.) the spatial extent of wild and stocked paddlefish movements and 3.) concomitant management implications of these survival and movements estimates.

MATERIALS AND METHODS

Data Set

The MICRA paddlefish stock assessment project encompasses the 20 state area that makes up the current distribution of paddlefish (Figure 5.1). Management regulations for paddlefish in the Mississippi River basin vary and range from being a protected species to one that is harvested both recreationally and commercially (Figure 5.1). The MICRA database is a compilation of data collected by cooperating states from 1995-present and contains morphometric information such as length and weight, as well as habitat information such as flow velocity and water quality where paddlefish were captured throughout the study area. Paddlefish were marked with an individually numbered coded wire tag (CWT; Northwest Marine Technologies, Shaw Island, WA) inserted in their rostrum at the time of capture during 1995-2007. Coded wire tags were located with a CWT detecting wand (Northwest Marine Technologies, Shaw Island, WA), cut out of the rostrum, and replaced with a new individually numbered CWT upon recapture. Coded wire tags were removed from the rostrum because the tag can only be decoded by reading a series of physical marks on the tag under a microscope. Recapture only collection (no new CWTs placed in wild caught fish) occurred from 2007-2009. Paddlefish were remarked with an individually numbered metal jaw tag during the recapture only period to differentiate previously marked from unmarked paddlefish.

The MICRA paddlefish database also contains hatchery release information from 1990-2009 on batch CWTed hatchery-origin paddlefish from 12 states: North Dakota, South Dakota, Kansas, Oklahoma, Texas, Missouri, Kentucky, Tennessee, Louisiana, New York, Pennsylvania, and West Virginia. The batch CWT was removed from

recaptured hatchery-origin paddlefish and replaced with either a new individually numbered CWT or a metal jaw tag.

Data Analysis

The MICRA database contains capture-recapture information obtained from >40 gear-types, thus hindering many standard fishery population dynamics analyses that require gear-specific catches to account for size selective gear bias. Therefore, we used multi-state mark recapture analyses (MSMR) (Hestbeck et al. 1991; Brownie et al. 1993) in Program MARK (White and Burnham 1999) to compute maximum-likelihood estimates of survival (S), recapture (ρ), and movement (ψ) probabilities. A benefit of this approach is that the ρ can account for unequal effort (Steffensen et al. 2010) allowing us to capitalize on the large amount of spatial and temporal data in this database despite the lack of gear consistency.

We determined if individual paddlefish were of hatchery or wild-origin from tagging information found within the database and assigned those origins to each fish for initial capture and all recaptures throughout its life. States are the current management unit of migratory fishes; however, the data in the MICRA database were too sparse to allow for informative state-specific analyses of S , ρ , and ψ . Instead, parameters S , ρ , and ψ were estimated among river basins as designated in the MICRA database (Figure 5.2): Gulf Basin (rivers that drain directly into the Gulf of Mexico), Missouri Basin (Missouri River and its tributaries), Mississippi Basin (Mississippi River and its tributaries excluding the Missouri and Ohio rivers), and Ohio Basin (Ohio River and its tributaries).

We conducted two different MSMR analyses: one using only wild-origin paddlefish and another analysis using only hatchery-origin paddlefish. Migratory fish in general are on the decline and an analysis of only wild origin paddlefish was meant to provide an initial large-scale estimate of population vital rates (S , ρ , and ψ). Additionally, paddlefish are stocked extensively throughout their range; population supplementation through stocking is becoming commonplace for species restoration and sport fish recovery plans. Cursory estimates of stocked paddlefish (e.g., S , ρ , and ψ) have not yet been computed that would allow for a better understanding of how these introduced fish are being incorporated into populations. The wild-origin analysis contains information from 1995-2009 (the duration of the MICRA project). The hatchery-origin analysis contains information from 1990-2009 because the MICRA project obtained mark-recapture information on hatchery-origin paddlefish beginning in 1990. Capture and recapture periods were designated as a calendar year running from 1 January to 31 December. Parameter estimates were obtained used a logit link function with constant time estimates of S , ρ , and ψ ; time-specific S , constant ρ , and constant ψ ; and constant S , constant ρ , and time-specific ψ . Each basin and time-step for S estimation represented one parameter in the models. Each pair-wise basin combination and time-step for ψ estimation represented one parameter in the models. We did not vary ρ by time because of highly variable fishing effort within a basin and we believe this warrants a more conservative approach than varying ρ by time would allow (Figure 5.3). Movement parameters (e.g., Missouri Basin to Mississippi Basin; Ohio Basin to Mississippi Basin, etc.) were fixed to zero when movement between basins was not recorded in the MICRA

database. Movement parameters that were fixed to zero in the wild fish MSMR analysis included the Gulf Basin to all basins (due to very limited hydrologic connection and lack of movement of recaptured fish), and the Missouri River Basin to the Ohio River Basin. Movement parameters that were fixed to zero in the hatchery MSMR analysis included the Gulf Basin to all basins, the Ohio River Basin to all basins, and the Mississippi River Basin to the Ohio River Basin. Models were ranked by Akaike's Information Criterion (AIC) where the model with the lowest AIC is the considered the best model.

RESULTS

A total of 22,688 wild paddlefish was marked from 1995-2009: 812 in the Gulf Basin, 6,339 in the Mississippi River Basin, 6,854 in the Missouri River Basin, and 8,683 in the Ohio River Basin (Figure 5.3). A total of 3,286 wild paddlefish was recaptured from 1995-2009: 29 in the Gulf Basin (3% recaptured), 565 in the Mississippi River Basin (8% recaptured), 1,759 in the Missouri River Basin (25% recaptured), and 933 in the Ohio River Basin (10% recaptured) (Figure 5.4).

The null model (time-constant model) had a lower AIC value than the time specific model and was selected as the sole best model (Table 5.1). Wild paddlefish had differential S , ρ , and ψ probabilities among basins. The Missouri River Basin had the highest S and ρ , while the Mississippi River Basin had the lowest S and the Gulf Basin had the lowest ρ (Table 5.2). However, the Gulf Basin also had very wide confidence limits about its S estimates and was not significantly different from the other basins (Table 5.2). Limited capture-recapture data from this basin does not allow it to be distinguished from other basins and did not have movement to or from this basin and its

parameter estimates will not be discussed further. The Ohio River Basin, Mississippi River Basin, and the Missouri River Basin, had S estimates that differed from each other as shown by the lack of overlap in 95% confidence intervals (Table 5.2).

Some wild paddlefish did move across basin boundaries, albeit with low annual ψ probabilities (Table 5.2). Paddlefish movements were generally confined within a river basin. However, interbasin movements were most common from the Missouri to Mississippi basin and the reciprocal and from the Mississippi to the Ohio basin, but not the reciprocal (Table 5.2).

A total of 2,226,421 marked paddlefish were stocked from 1990-2009: 1,059,375 in the Gulf Basin, 181,150 in the Mississippi River Basin, 851,856 in the Missouri River Basin, and 134,040 in the Ohio River Basin (Figure 5.5). A total of 1,362 hatchery origin paddlefish were recaptured from 1990-2009: 331 in the Gulf Basin (0.03% recaptured), 239 in the Mississippi River Basin (0.1% recaptured), 784 in the Missouri River Basin (0.09% recaptured), and 8 in the Ohio River Basin (0.006% recaptured) (Figure 5.6). Survival, ρ , and ψ estimates for stocked paddlefish where estimates were held constant over time were not produced because the results suggested that the model did not converge. For instance, several estimates contained either very large 95% confidence estimates (e.g., $<0.1^{-10}$ to nearly 1.0), or suspiciously tight 95% confidence estimates (e.g., 1.0 to 1.0), given the small amount of recapture information in the MICRA database. Therefore, we did not further parameterize models to obtain estimates.

DISCUSSION

The best basin-level estimates of S , ρ , and ψ were not time-specific so the information obtained from the MICRA database should be interpreted as average annual S , ρ , and ψ probabilities across the basin over the study period. This broad-scale set of estimates, while not necessarily useful for examining time-sensitive phenomenon such as response to flow regimes, or scale-sensitive phenomenon such as changes in short-term management, does allow a first attempt at evaluating vital rates for a migratory species at a nearly range-wide scale. This broad-scale study therefore provides insights into pertinent questions that should help direct future research and management objectives (e.g., what are causes of differing mortality among basins, how many paddlefish can be sustainably harvested, what causes differential movement rates among basins, are there source-sink population dynamics occurring at a large-scale). Moreover, a greater understanding of migratory fish may help focus management and research resources to areas with the greatest needs.

Survival rates are highest in the Missouri River Basin ($S=0.86$), the only basin among the Mississippi, Missouri, and Ohio basins without commercial harvest (Table 5.1). While there is recreational harvest within each basin, the greater S estimates may be an indicator of relatively high commercial harvest mortality in the Mississippi and Ohio basins. Further examination of the causes of differing S probabilities through continued contribution of data to the MICRA database, examination of the data in the MICRA database, and focused local efforts is warranted to more fully tease apart causes of differing S probabilities among basins.

Sampling effort from 1990-2009 has been inadequate to provide reliable estimates

of S , ρ , and ψ probabilities for stocked fish. Large numbers (>2 million) of stocked paddlefish have been released during the MICRA project (1990-2009) and our inability to obtain useful estimates from these data suggest that we are not effectively monitoring these fish. Stocking records like those in the MICRA database are unparalleled at such a large spatial scale. Estimates like those we attempted here for stocked paddlefish are not yet reliable enough to estimate S or ψ for due to small proportions of recaptures, thus emphasizing the need for increased sampling.

Paddlefish are primarily considered a sport fish in many states throughout their range (Figure 5.1), thus considerations typically reserved for stocking species of conservation concern, such as careful consideration of broodstock genetics, have not always been employed. Understanding how stocked migratory fish are incorporated into populations can help managers create more effective management strategies. For instance, a study examining marked and recaptured stocked pallid sturgeon was able to provide insight into what stocking strategies are most effective (Steffensen et al. 2009). However, as a better understanding of large-scale movements is gained and declines in populations of migratory fish species continue, it may be necessary to more accurately evaluate, monitor, and reconsider stocking strategies that benefit life-history needs than those at scales larger than state-specific management can provide.

Movement into and out of river basins suggests that current migratory fish management conducted on a state-specific basis may not be of a sufficient spatial-scale to effectively manage migratory fish populations. Anecdotally, there are several accounts

within the MICRA database of movement of paddlefish between states, sometimes between states with different management objectives (e.g., moving from a state where they are protected to a state with commercial or sport harvest and vice versa). Within a basin, and sometimes between bordering states, there can be incongruous management regulations and conservation statuses (Figure 5.1). The bounds of the movements of migratory fishes such as paddlefish can exceed the spatial reach of a state's management actions, potentially exerting multiple management efforts on a population simultaneously. The potential paradox created by the mis-match of management and conservation strategies is largely unknown for migratory freshwater fishes. However, other migratory fish species like blue sucker (Neely et al. 2009), sauger *Sander canadense* (Pegg et al. 1997; Graeb et al. 2009), and pallid sturgeon (Steffensen et al. 2009) have been documented to make interjurisdictional movements and may also be exceeding the spatial reach of state-specific management.

CONCLUSIONS

Riverine biodiversity is declining at high rates due to a number of factors (Allen and Flecker 1993; Dudgeon et al. 2006; Vorosmarty et al. 2010) and migratory fish are particularly vulnerable to these declines due to habitat alterations that have interfered with key life history events like migrations (Peter 1998). Current and future threats to migratory fishes including habitat loss, blocked migrations, commercial and sport overharvest, invasive species, and climate change create a great need for assessing the viability of interjurisdictional cooperation to address problems at the appropriate scale.

Long-range movements by freshwater migratory fishes can leave populations subject to several different management objectives simultaneously that can potentially interfere with the ability of any one state from accomplishing their management and/or conservation objectives when populations are influenced beyond jurisdictional boundaries. Some interjurisdictional cooperation in management and recovery efforts do exist (Argent et al. 2009; Mestl and Sorensen 2009), so larger scale cooperation is possible. Increasing numbers and intensity of cooperative interjurisdictional efforts, as exemplified by the MICRA project, may aid in balancing transitions between state-specific management and larger cooperative frameworks that manage freshwater migratory fishes at biologically relevant spatial scales.

The conventional approach to management of migratory freshwater fishes has been through state-specific control. However, considerations of a biologically relevant management framework that can accommodate the large-scale movements of migratory fish species may be appropriate to buffer species against current and future threats. The use of movements to determine biologically relevant boundaries for interjurisdictional management is not new to wildlife management; migratory waterfowl have been managed through federal and state cooperation through migratory waterfowl flyway councils since 1949 (USFWS 2010). Migratory waterfowl, for instance, have a broad set of restrictions set by interjurisdictional flyway councils, the federal government, and states. States are afforded local control of regulations within the confines set by the interjurisdictional governing body and while a state can be more restrictive than the federal regulations for the flyway, they cannot be less restrictive. Similarly, movements

of paddlefish and possibly other migratory fishes could be used to set management boundaries and we show one possible example for interjurisdictional management of paddlefish based on our analyses (Figure 5.7). The management units largely represent basin-specific areas, connecting basins that contain most of the recorded movements of paddlefish. Our spatial configuration example for management of paddlefish could also be applied to other migratory fishes when and where movement or other vital population data are available. However, the framework should be tailored to fit specific species or community needs to provide a spatial framework for a cohesive management strategy.

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Table 5.1. Competing models for survival (S), recapture (ρ), and movement (ψ) of wild paddlefish across their range in the greater Mississippi River Basin of the USA from 1995-2009. Models were ranked by Akaike's information criteria (AIC), and parameter abbreviations are as follows: k is the number of parameters, ΔAIC is the difference between AIC values from each model, and w_{AIC} is the Akaike weight (all weights sum to 1). Models included survival as time-specific (S_t) or constant ($S.$), recapture probability as constant ($\rho.$), and movement as time-specific (ψ_t) or constant ($\psi.$).

Model	k	AIC	ΔAIC	w_{AIC}
$S., \rho., \psi.$	12	17,231.53	0.00	1.00
$S_t \rho., \psi.$	20	17,249.06	17.53	0.00
$S., \rho., \psi_t$	26	17,504.91	273.38	0.00

Table 5.2. Survival (S), recapture (ρ), and movement (ψ) probability (95% confidence estimates) by river basin for wild paddlefish in the Mississippi Interstate Cooperative Resource Association Paddlefish Stock Assessment Database from 1995-2009. Survival and recapture estimates are given on the diagonal and movement estimates between basins are given on the off-diagonal. Basins listed on rows are originating basin of movement and basins listed on columns are basins receiving fish.

Basin	Gulf	Missouri	Mississippi	Ohio
Gulf	S= 0.78 (0.55-0.91) $\rho = 0.002$ (0.0007-0.005)	0	0	0
Missouri	0	S= 0.86 (0.84-0.88) $\rho = 0.03$ (0.026-0.032)	$\psi = 0.001$ (0.002-0.007)	0
Mississippi	0	$\psi = 0.001$ (0.00018-0.009)	S=0.64 (0.59-0.69) $\rho = 0.009$ (0.007-0.13)	$\Psi = 0.007$ (0.003-0.017)
Ohio	0	$\psi = 0.0006$ (0.00016-0.003)	$\psi = < 0.0001^*$	S=0.79 (0.75-0.82) $\rho = 0.07$ (0.009-0.01)

*95% confidence interval encompasses 0

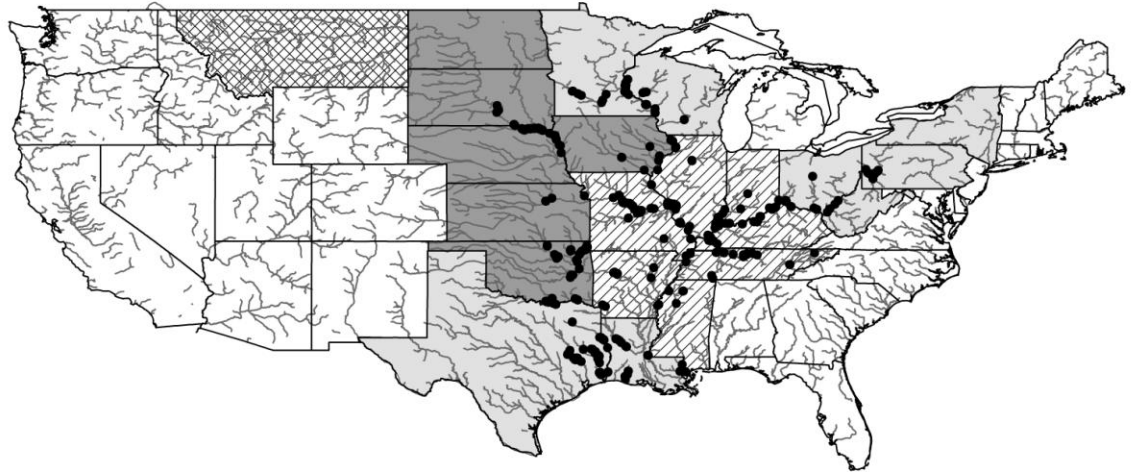


Figure 5.1. Map of collection sites as included in the Mississippi Interstate Cooperative Resource Association paddlefish stock assessment database from 1995-2009.

Conservation and harvest status of paddlefish in each state is indicated by shading: no harvest due to state threatened, species of concern, or protected (light gray); species of special concern and sport harvest (crosshatch); sport harvest (dark gray); sport and commercial harvest (diagonal hatch). Conservation and harvest status obtained from Betolli et al. (2009).

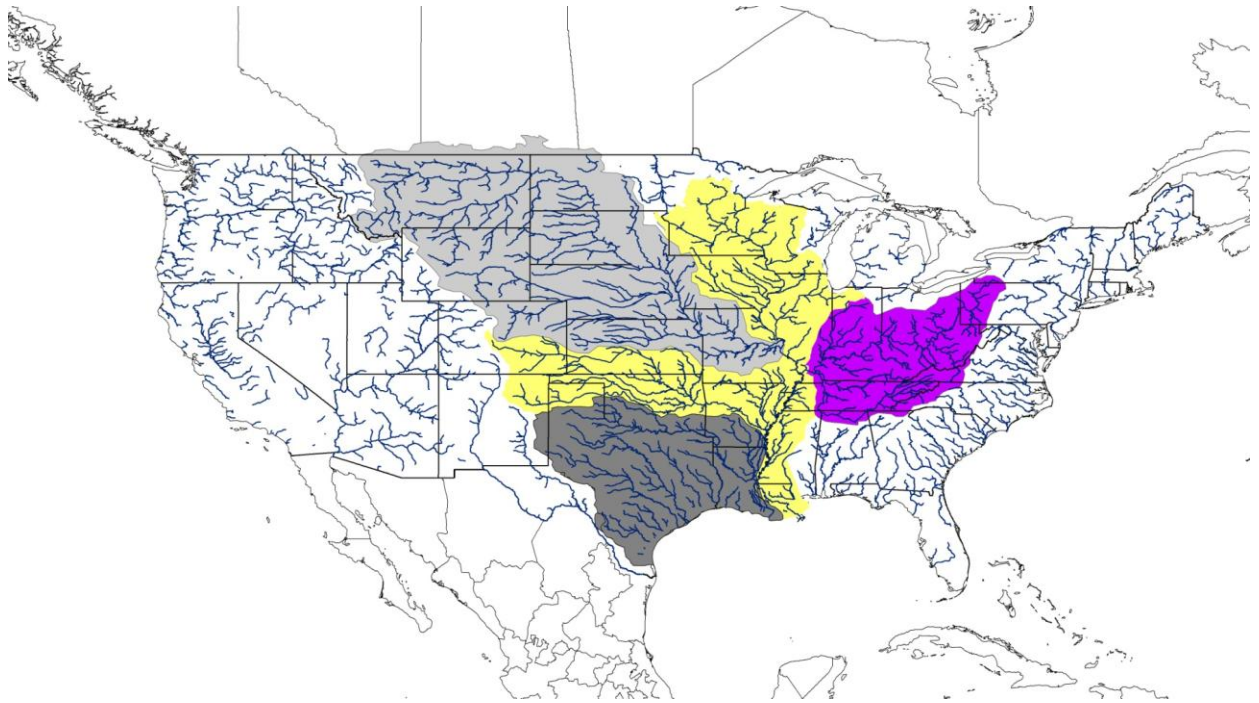


Figure 5.2. Map of river basins as designated in the Mississippi River Interstate Cooperative Resource Association Paddlefish Stock Assessment Database. Shaded areas represent basins as follows: light gray—Missouri River Basin, yellow—Mississippi River Basin, dark gray—Gulf Basin, purple—Ohio River Basin.

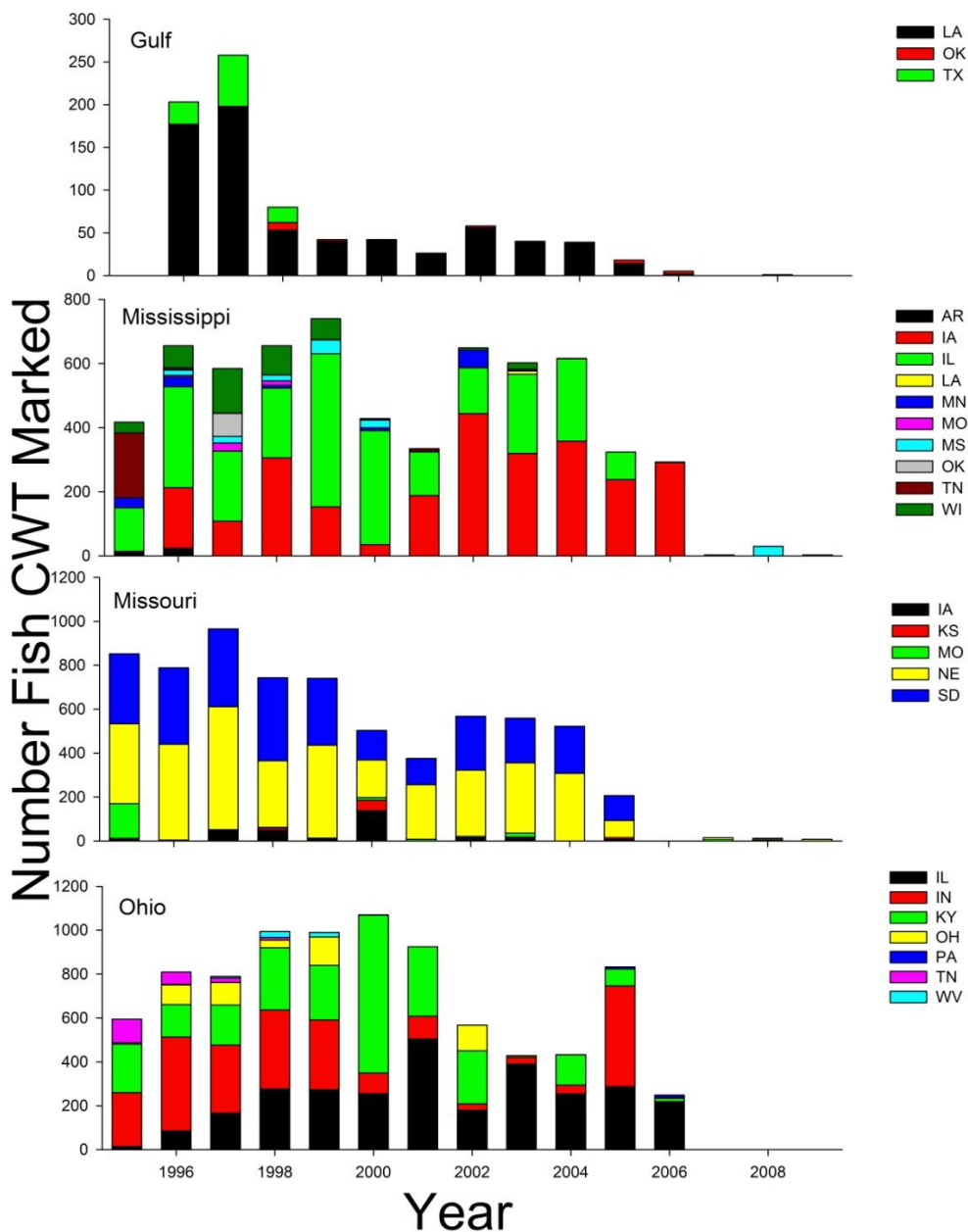


Figure 5.3. Number of paddlefish marked by coded wire tag (CWT) in each basin by state irrespective of gear type in the Mississippi River Interstate Cooperative Resource Association Paddlefish Stock Assessment Database from 1995-2009. Note the differences in y-axis scales.

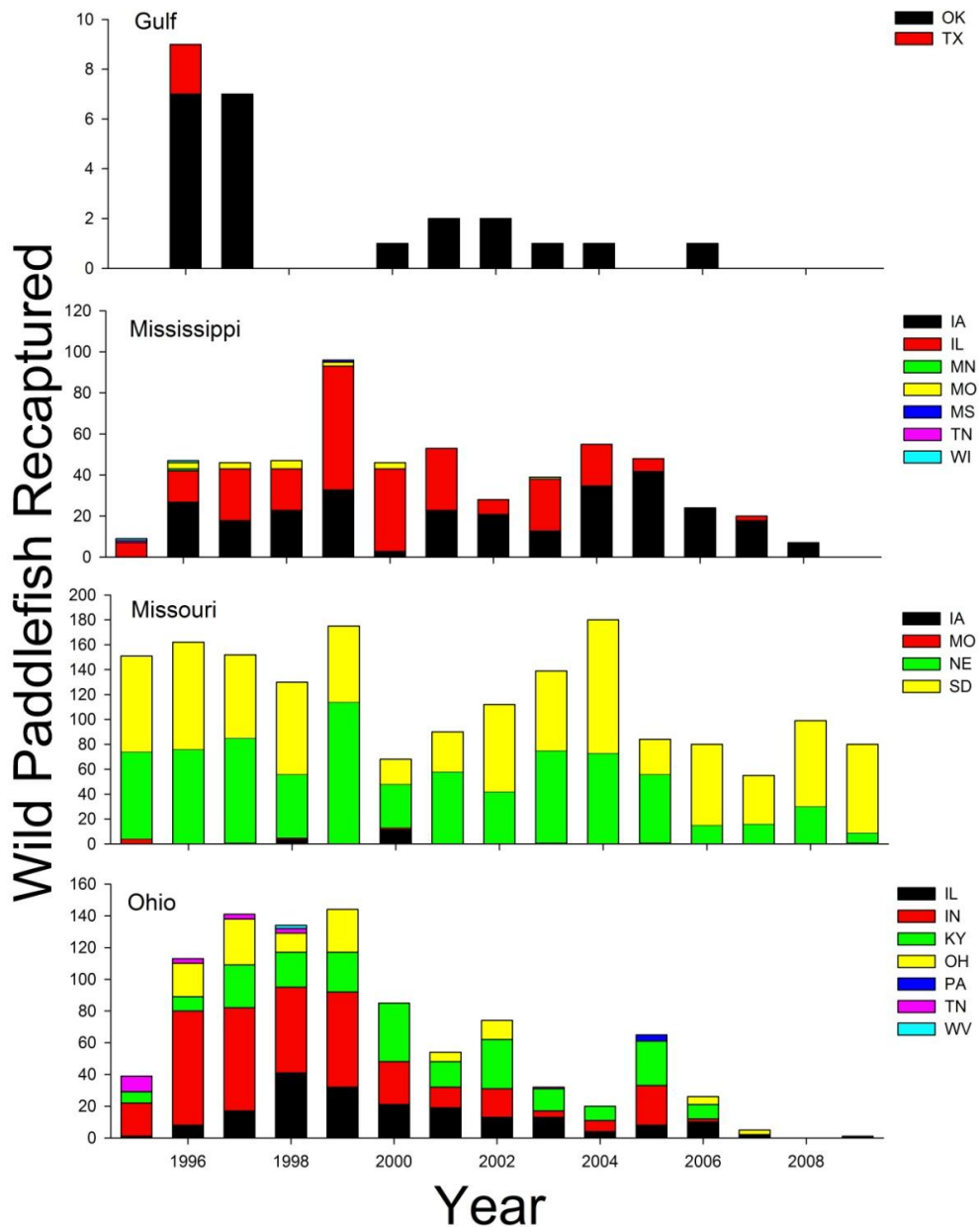


Figure 5.4. Number of wild paddlefish recaptured with coded wire tags in each basin by state irrespective of gear type in the Mississippi River Interstate Cooperative Resource Association Paddlefish Stock Assessment Database from 1995-2009. Note the differences in y-axis scales.

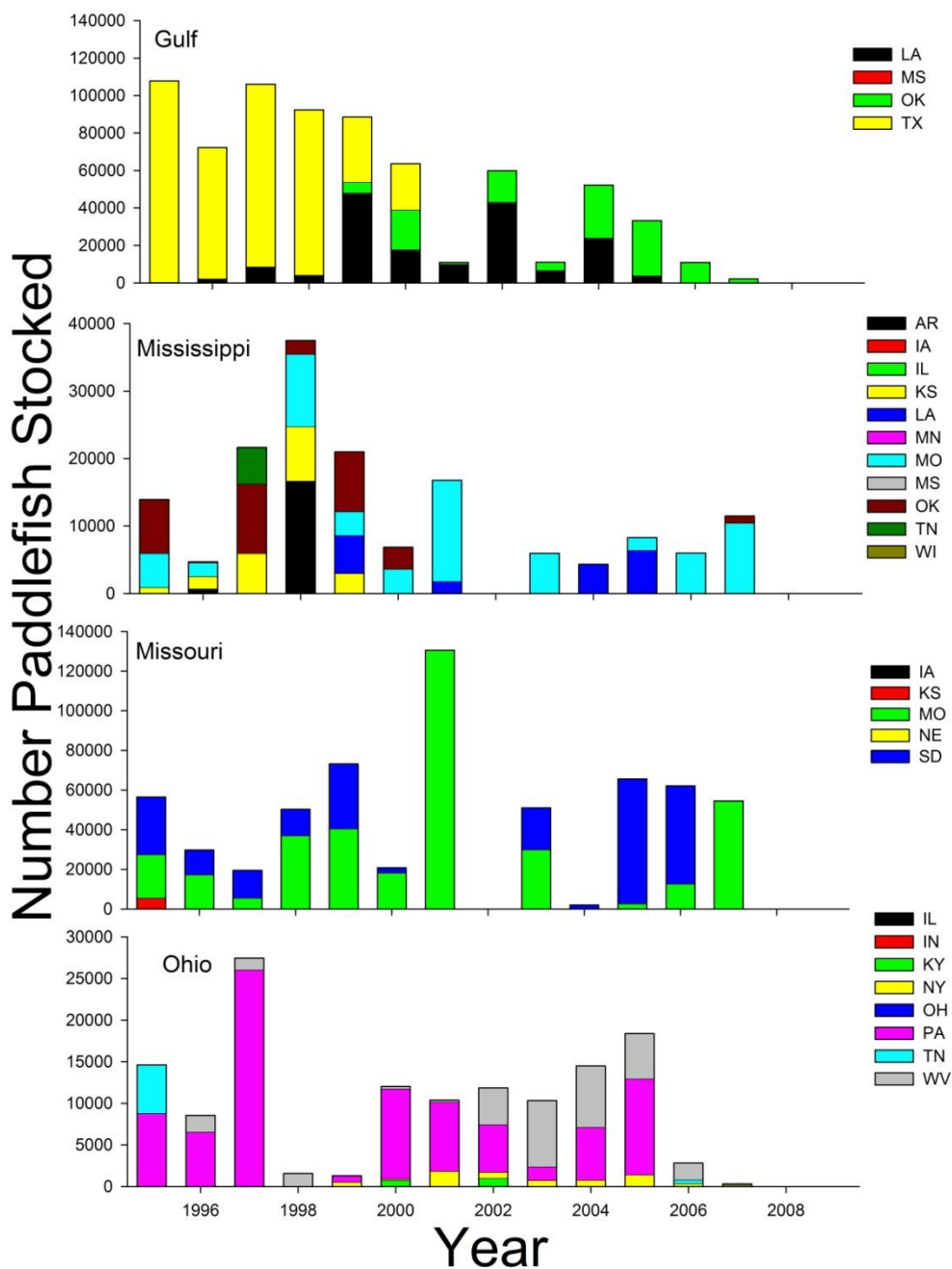


Figure 5.5. Number of paddlefish stocked in each basin by state in the Mississippi River Interstate Cooperative Resource Association Paddlefish Stock Assessment Database from 1995-2009. Note the differences in y-axis scales.

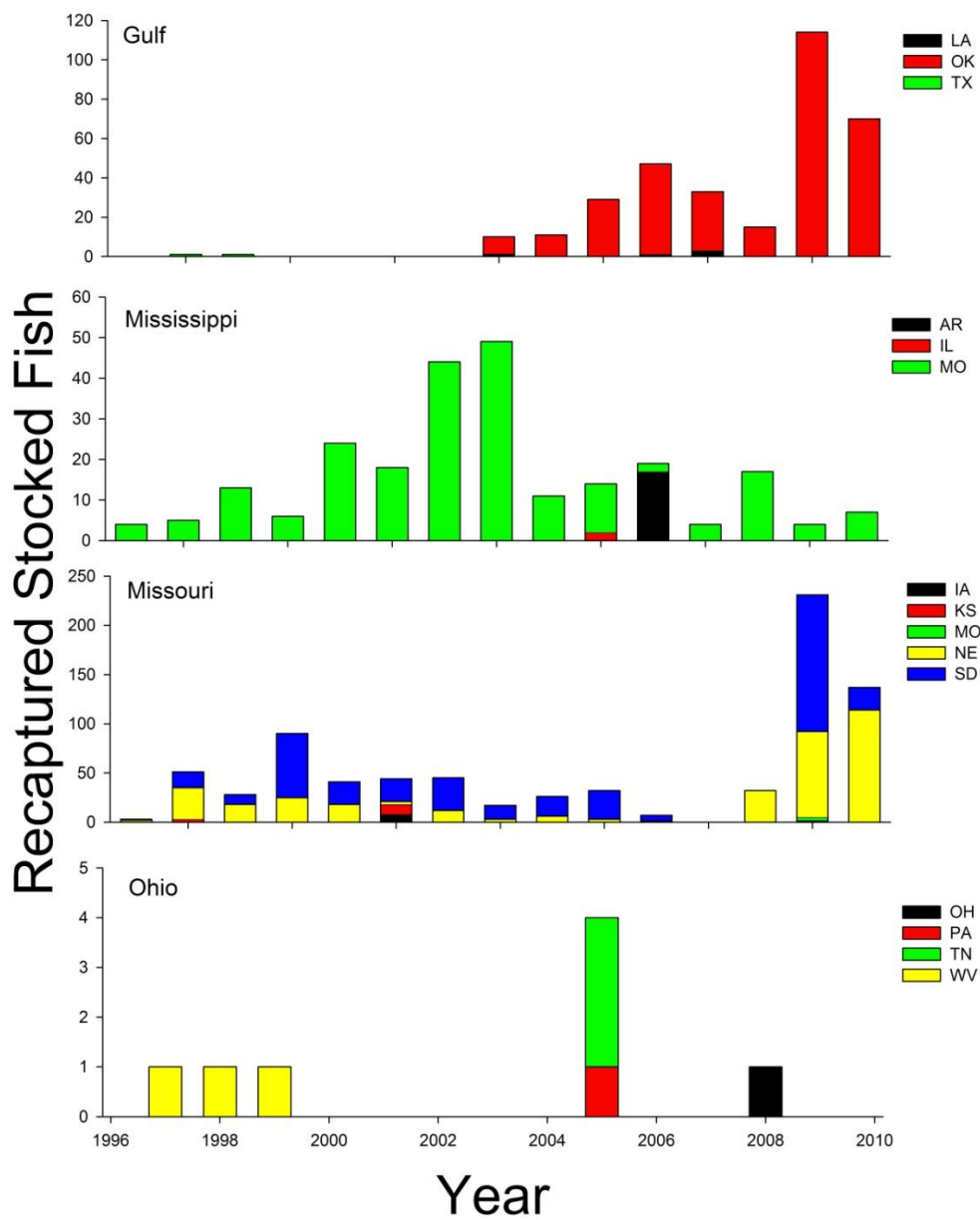


Figure 5.6. Number of stocked paddlefish recaptured with coded wire tags in each basin by state irrespective of gear type in the Mississippi River Interstate Cooperative Resource Association Paddlefish Stock Assessment Database from 1995-2009. Note the differences in y-axis scales.

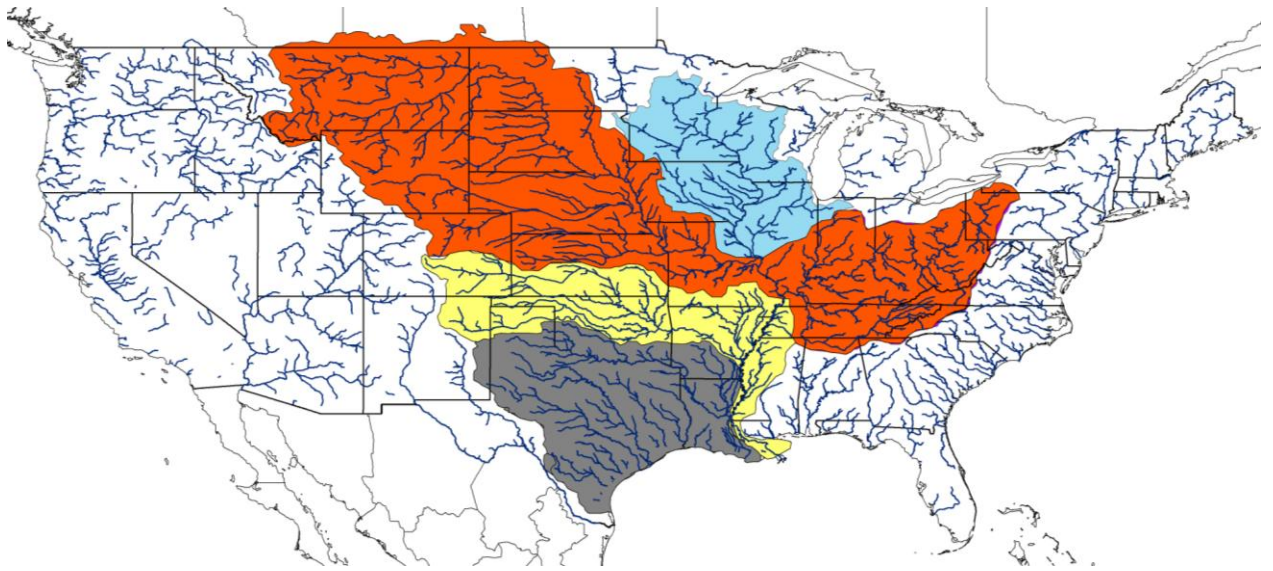


Figure 5.7. Potential interjurisdictional management spatial framework determined using paddlefish movements to set management boundaries. The orange shaded area represents the Missouri-Middle Mississippi-Ohio river basin unit, the blue shaded area represents the Upper Mississippi River Basin management unit, the yellow shaded area represents the Lower Mississippi River Basin management unit, and the gray shaded area represents the Gulf of Mexico Basin management unit.

CHAPTER 6: CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

The global plight of sturgeon and paddlefish underscores the urgency for measures that increase the probabilities of species persistence. However, because paddlefish are not listed as a federally endangered species, monetary limitations restrict the ability of many states to effectively or extensively monitor their paddlefish populations. Paddlefish are a highly migratory species that frequently traverse state boundaries, and as such, have a need for interjurisdictional cooperation including agreement on certain species conservation and management goals among management agencies. Stocked paddlefish, a group of fish that only exists as a result of a management action, for example, are able to undergo extensive movements, even when stocked in reservoirs, thus carrying management actions across state lines (Chapter 5). Additionally, paddlefish life histories have the potential to be influenced by harvest regulations by a state, and the migratory nature of these fish potentially inhibit the ability of states to manage their paddlefish populations in a predictable way (Chapters 4 and 5). Large database resources, such as the MICRA Paddlefish Stock Assessment Database do not exist for other species of Acipenserid fishes or other species of potamodromous riverine fishes, so similar, large-scale analyses of movements such as those in Chapter 5 for paddlefish may not be possible. The rarity of the MICRA Paddlefish Stock Assessment Database underscores the need to use this database as a tool to better understand freshwater migratory fishes and potential impacts of their management and create better solutions for their conservation and management.

The future of conservation for potamodromous riverine fishes may lie with using river sub-basins or a combination of river sub-basins to delineate management units.

Within these management units, large river tributaries may be integral to species conservation and restoration plans (Chapter 2). Stocking must be used carefully in species conservation and restoration plans on both a local and range-wide scale. For example, stocked paddlefish from Lake Francis Case now comprise >40% of the currently unstocked population immediately downstream of Fort Randall Dam. Stocked paddlefish below Fort Randall Dam also have reduced genetic diversity compared to wild individuals (Sloss et al. 2009); a phenomenon that has been reported for paddlefish in other populations across their range (Epifanio et al. 1998) and in other species of fishes (Jorgensen et al. 2007).

In light of the work presented in this dissertation, I make the following management recommendations (by chapter):

CHAPTER 2: TRIBUTARIES INFLUENCE RECRUITMENT OF FISH IN LARGE RIVERS

- Natural flow regimes that still exist in tributaries to large, altered rivers are important for populations of large river endemic fishes. For example, the Niobrara River, a tributary to the Missouri River with a largely unaltered flow regime, has been found to be an important predictor of not only paddlefish recruitment, but also other sport fish like sauger *Sander canadense* and walleye *S. vitreum* recruitment in the Missouri River. Maintaining the current, relatively unaltered flow regime on the Niobrara River is imperative to protecting fish populations between Ft. Randall and Gavins Point dams.
- Monitoring of young-of-year paddlefish through the Lewis and Clark Lake paddlefish trawl that has been ongoing from 1965-present should be continued

because it provides a useful metric for measuring natural reproduction and aid in understanding fish population trajectories for the reach of river between Ft. Randall and Gavins Point dams.

- The contribution of fish stocked above Ft. Randall Dam to waters below Ft. Randall Dam should be evaluated. Specifically, natural reproduction of paddlefish does occur between Ft. Randall and Gavins Point dams and whether or not stocked paddlefish are influencing this natural reproduction is not known. Therefore, addressing if entrainment of stocked paddlefish through Ft. Randall Dam is leading to density-dependent reproductive suppression of the paddlefish population between Ft. Randall and Gavins Point dams is warranted.

CHAPTER 3: MOVEMENT AND HABITAT USE OF WILD AND STOCKED PADDLEFISH: IMPLICATIONS FOR SPECIES RESTORATION AND CONSERVATION

- Further evaluation of movement and habitat use of wild and entrained stocked paddlefish between Ft. Randall and Gavins Point dams is needed to determine if there are any behavioral differences between wild and stocked paddlefish. Specifically, meso- and micro-habitat use should be evaluated to determine if differences in variables such as choice of flow velocities exist that may equate to differences in energy expenditures that could scale up to differences in population metrics (e.g., fecundity, longevity, etc.) between wild and stocked paddlefish.

- This study did not find differences between movement and habitat use of wild and stocked paddlefish. It is possible, because they appear to be behaviorally equivalent, that wild and stocked paddlefish are breeding or could do so in the future. Interbreeding of wild and stocked paddlefish could lead to genetic introgression, or reduced genetic diversity of the wild population (as has been shown for other species of fish) underscoring the importance of genetic monitoring of wild and hatchery-origin individuals in this population.

CHAPTER 4: POPULATION CHARACTERISTICS OF PADDLEFISH BETWEEN FT. RANDALL AND GAVINS POINT DAM ON THE MISSOURI RIVER

- Continued monitoring of paddlefish populations below Fort Randall Dam, including the population below Gavins Point Dam, to determine the trajectory of the wild population, and the continued contribution of entrained, stocked paddlefish that has the potential to influence these paddlefish populations well into the future due to the longevity of paddlefish.
- Comparisons of wild and stocked paddlefish survival and entrainment rates through continuation of mark-recapture studies can aid in understanding of the trajectory of the paddlefish population between Ft. Randall and Gavins Point dams and below Gavins Point Dam. Studies that examine potential differences between wild and stocked paddlefish are important because of the growing body of literature suggesting that wild and stocked fish in the same population differ in characteristics such as genetic diversity, fecundity, movements, etc.

- Determine if wild and hatchery-origin paddlefish are interbreeding and if they are, if their progeny have incurred loss of genetic diversity that may have phenotypic correlates that impact fitness (e.g., survival, fecundity, spawn timing, etc.).
- Further genetic assessment and continued genetic monitoring of paddlefish populations downstream of Fort Randall Dam are needed, particularly the reach between Ft. Randall and Gavins Point dams, to determine population-level genetic effects such as inbreeding depression or genetic introgression that may have occurred or can occur as a result of long-term stocking of large numbers of paddlefish.
- Extensive efforts, such as careful selection of only wild-origin broodstock based on genetics, need to be made to ensure genetic integrity of the local paddlefish population is preserved.
- Careful monitoring of the paddlefish population downstream of Gavins Point Dam to determine the contribution of entrained hatchery-origin paddlefish from Lake Francis Case and the potential impacts if stocking is ended.
- Re-evaluate the number of paddlefish stocked in Lake Francis Case given the large numbers of paddlefish that are being entrained.
- Validation of paddlefish ageing techniques is important to understanding the accuracy and precision of this approach in addition to the interpretation of jawbone ageing data. We have a unique opportunity between Ft. Randall and Gavins Point dams to validate jawbone ages of relatively old (\geq age 20)

paddlefish. There was discrepancy in reader assigned ages in this study as well as between reader assigned ages and known age, although on par with that reported by other studies (Scarnecchia et al. 2007; Pierce 2010). Future studies that seek to increase the accuracy of ageing using this population containing many known age paddlefish could be helpful to paddlefish researchers throughout the USA so that building in tolerances for error (Scarnecchia et al. 2007) would not be needed.

CHAPTER 5: INCREASED MANAGEMENT SPATIAL EXTENT AND MONITORING EFFORTS ARE NEEDED FOR FRESHWATER MIGRATORY FISHES

- Re-thinking current, conventional management strategies to incorporate more interjurisdictional cooperation to include a broader spatial extent is necessary to help accomplish species management and conservation objectives. Having a comprehensive stocking plan, commercial and recreational harvest, and assessment program would help conserve the resource, yet hopefully keep it a viable renewable resource.
- Paddlefish undergo large-scale movements; however, we do not yet understand the nature of these connections (e.g., whether these connections tie populations together biologically or genetically). Current technologies and paddlefish genetic data do not yet provide adequate resolution of the nature of these population connections, but future studies should seek to establish the nature of these connections as improved technology becomes available. Increasing coverage of genetic data coupled with continued mark-recapture

efforts for this species may help to establish thresholds for biologically meaningful population connections.

- Current monitoring efforts do not appear to provide adequate information to understand vital rates of stocked paddlefish, if those vital rates differ from wild paddlefish, or how stocked paddlefish are being incorporated into populations. Therefore, rigorous evaluation of range-wide stocking activities is necessary including site selection, numbers of fish being stocked, genetic monitoring, and monitoring of stocked populations in addition to populations downstream of stocked populations.
- Gain a better understanding of the sources of mortality among basins including habitat loss and alteration, recreational and commercial harvest mortality, loss of natural flow regimes, turbine strike and other hydropower injuries, commercial navigation. These several potential sources of mortality may have varying effects in each river basin and it is important to understand how these factors influence population dynamics to continue conserving paddlefish as a natural resource.

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APPENDIX A: PADDLEFISH LIFE HISTORY

Population declines and extirpations have sparked numerous studies to elucidate various aspects of paddlefish life history. Male paddlefish attain reproductive maturity between ages 4 and 9 at an average weight of 12.7-kg; whereas, females mature between ages 6 and 12 at an average weight of 18.7-kg (Jennings and Zigler 2009). Males are thought to spawn each year; however, some studies report that females may only spawn every 2 to 5 years (Jennings and Ziegler 2009) and Meyer (1960) estimated that female paddlefish only spawn every 4 to 7 years based on dentary bone analysis. Long periods between female spawning events are likely due to the large reproductive energy investment as mature egg masses can comprise up to 25% of body weight (Purkett 1961).

Paddlefish spawn on hard substrates in areas with sufficient current to prevent sediment deposition over eggs (Alexander 1914; Purkett 1961; Ruelle and Hudson 1977; Pasch et al. 1980; Wallus 1986). Paddlefish typically spawn during spring when water level rises serve as a spawning cue (Russell 1986) for upstream spawning migrations (Robinson 1966; Rehwinkel 1978; Pasch et al. 1980; Southhall and Hubert 1984; Lein and DeVries 1988; Paukert and Fisher 2001; Stancill et al. 2002; Firehammer and Scarnecchia 2006). Paddlefish usually migrate downstream after spawning (Russell 1986; Paukert and fisher 2001; Stancill et al. 2002; Firehammer and Scarnecchia 2006).

The 2-4-mm eggs (Larimore 1950; Purkett 1961) adhere to the first surface they contact after fertilization (Purkett 1961) and hatch in 6 to 14 days, depending on water temperature (Purkett 1961; Graham 1986). Paddlefish emerge from eggs as 8.5-mm total

length (TL) larvae (Purkett 1961; Pasch et al. 1980) and begin selectively feeding on zooplankton and insects (Ruelle and Hudson 1977) after yolk-sac absorption at approximately 17-mm TL (Jennings and Zigler 2009). Young paddlefish continue to feed on zooplankton and insects until approximately 120 to 250-mm TL (Ruelle and Hudson 1977; Rosen and Hales 1981; Michaletz et al. 1982) when the gill rakers become sufficiently developed to allow a switch to filter feeding.

Larval and juvenile paddlefish (pre-reproductive paddlefish >160 mm TL) habitat use varies with age (Jennings and Zigler 2009). Larval paddlefish are uniformly distributed across the river channel, likely due to insufficient muscle and fin development to move to preferred habitat (Wallus 1986). Post-yolk sac larvae congregate in benthic environments of a river channel during the day and move near the water surface at night (Wallace 1986). Young-of-year (YOY) paddlefish are typically suspended near the bottom of the main river channel in large schools (Ruelle and Hudson 1977). Movements and habitat use becomes more similar to that of adult paddlefish as juvenile paddlefish age (Pitman and Parks 1994; Hoxmeier and DeVries 1997).

Historic and present-day adult paddlefish habitat use differs dramatically. Optimal paddlefish habitat once consisted of slower-moving side channels and oxbow lakes (Stockard 1907, Alexander 1914), but impoundment and channelization of rivers cut off oxbow lakes and eliminated backwater and side-channel areas. These alterations have driven paddlefish to inhabit riverine areas in search of slower current velocities that can occur in dam tailwaters and tributary mouths (Rosen 1976; Southhall and Hubert 1984; Moen et al. 1992).

Adult paddlefish habitat selection also varies seasonally. Paddlefish often congregate in tailwater areas of dams in spring due to blocked upstream movements to spawning locations (Jennings and Zigler 2009). Unkenholz (1982) found that paddlefish inhabited tailwater areas throughout the summer months after spawning. Winter habitats of paddlefish are typically areas with slow current and depths > 3 m (Rosen et al. 1982).

Effects of reservoir aging on paddlefish are not well understood, but the nature of changes caused by this process could likely impact paddlefish populations. Reservoir aging causes sediment aggregation in reservoirs, particularly in headwater portions, thus reducing reservoir depths and changing geomorphology (Kimmel and Groeger 1986). Geomorphological changes translate into changes in habitat; perhaps destroying or creating spawning habitat or rearing grounds for a given species. Additionally, shifts in nutrient and biogeochemical cycling caused by reservoir aging can lead to changes in prey availability and abundance (Kimmel and Groeger 1986). Therefore, changes to managed lotic systems engendered through reservoir aging could influence paddlefish population ecology and dynamics by increasing or decreasing juvenile or adult survivorship and changing daily, seasonal or spawning movement patterns.

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