2006

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Recommended Citation

Graeb, Brian D. S., "Sauger Population Ecology in Three Missouri River Mainstem Reservoirs" (2006). *Electronic Theses and Dissertations*. 438.
https://openprairie.sdstate.edu/etd/438

Sauger Population Ecology in Three Missouri River Mainstem Reservoirs

By

Brian D. S. Graeb

A dissertation submitted in partial fulfillment of the requirements for the degree

Doctor of Philosophy

Major in Biological Sciences

South Dakota State University

2006

Sauger Population Ecology in Three Missouri River Mainstem Reservoirs

This dissertation is approved as a credible and independent investigation by a candidate for the Doctor of Philosophy degree and is acceptable for meeting the dissertation requirements for this degree. Acceptance of this dissertation does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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Acknowledgements

I would like to especially thank my wife, Stephanie for her support and guidance in all aspects of my life during my long tenure as a graduate student, and my advisor, Dr. David Willis for his patient guidance and sage advice, and for broadening my perspective as I develop into a scientist and teacher. Dr. Steve Chipps provided many hours of intellectual discussion, theoretical debates, and career advice; for the sake of the ivory-billed woodpecker I hope that I do not owe him $10 in 2015. Dr. Michael Brown challenged my approach to statistics and pushed me to the edge of quantitative thinking, and in the process broadened my approach to science. I would also like to thank Dr. Brian Blackwell and John Lott for guidance and logistical support. Neil Billington and Rachel Koigi conducted the genetic analyses for this project. I would like to thank many technicians and graduate students who made this research possible including: Jessica Roddy, Benjamin Temple, Dan Fjeld, Jamie Shepherd, Quentin Phelps, Matt Ward, Trevor Selch, Matt Mangan, and Chris Hoagstrom. Special thanks go to Mark Kaemingk and Michael Weber who not only excelled as technicians but developed into colleagues. Lastly, I would like to thank my family for steering me down this path and supporting me along the way. Partial funding for this research was provided by the South Dakota Game, Fish and Parks through Federal Aid in Sportfish Restoration funds (Federal Aid Project F-15-R, Study 1594) and by South Dakota Agricultural Experiment Station at South Dakota State University.

Abstract

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Brian D. S. Graeb

27 June 2006

Sauger *Sander canadensis* populations have experienced widespread declines across much of their range. Factors suspected to contribute to these declines include hybridization, exploitation, loss of spawning areas, and general habitat alterations associated with regulated rivers. Several sauger populations within the Missouri River basin are also experiencing similar declines, particularly in the headwaters of Montana, and the lower basin states of Nebraska and Missouri. However, sauger populations in many of the reservoirs in South Dakota (between Montana and the lower basin) have relatively stable populations. Given the paucity of information on factors influencing sauger population ecology in general, and Missouri River populations in particular, I studied several aspects of sauger population ecology in three Missouri River reservoirs to better understand factors influencing population structure. I focused on three primary research areas during the course of this study: 1) natural hybridization of sauger with walleye *Sander vitreus*, 2) sauger spawning habitat use in reservoirs, and 3) population dynamics of gizzard shad *Dorosoma cepedianum*, the primary prey fish for sauger in these systems. Results from this study will hopefully contribute to the understanding of sauger ecology and facilitate the advancement of conservation efforts.

Walleye and sauger naturally hybridize in many populations, but factors influencing hybridization are not completely understood. I genetically identified and determined relative year-class strength for 1,454 sauger, walleye, and naturally produced hybrids from three Missouri River reservoirs (Lakes Sharpe, Francis Case, and Lewis and Clark) to examine patterns of hybridization, and to quantify factors influencing year class formation. Hybridization rates varied from 4% in Lakes Sharpe and Francis Case to 21% in Lewis and Clark Lake. Hybrids comprised several year classes in each system indicating that hybridization does not occur in erratic pulses, but rather at a consistent low-level recruitment rate. Hybridization was directionally biased toward walleye as 60-72% of hybrids in each system were walleyes backcrossed with sauger genes. Year-class strength of sauger, walleye, and hybrids varied among reservoirs and species within reservoirs. Neither year-class strength of hybrids nor walleye was correlated with that of sauger, indicating that dissimilar factors influence year-class strength among hybrids and pure parental walleye and sauger. As such, recruitment modeling was scaled at individual species and hybrids and within individual reservoirs. Because Lake Francis Case had a low sample size of cohorts to model (few individuals >age 5) this system was excluded from recruitment modeling. Factors affecting recruitment of hybrids in Lewis and Clark Lake and parentals in both Lakes Sharpe and Lewis and Clark shared the common positive influence of warmer water temperatures during fish early life history, but recruitment differed among species and systems with regard to the effect of flow. Increased flow, either from mainstem cumulative discharge (hybrids) or tributary inputs (parentals), was negatively associated with year-class strength in my models for Lewis and Clark Lake, whereas tributary inputs and discharge were not well supported in models for sauger in Lake Sharpe (although tributary input warrants further investigation for walleye). The effect of flow on recruitment of sauger and walleye in Lewis and Clark Lake was confounded by an interaction with temperature. Tributary inputs negatively affected recruitment of sauger and walleye when water temperatures were reduced, but the effect of tributary input was negated during warmer years. Thus, these models suggest that higher than average recruitment can be expected during years with warmer spring/early summer water temperatures in Lakes Sharpe and Francis Case, and during years when flow (either from mainstem discharge for hybrids, or tributary inputs for sauger and walleye) are reduced in Lewis and Clark Lake.

To determine sauger spawning habitat in Lewis and Clark Lake, I attached 50 radio transmitters to pre-spawn, adult sauger during 2003 in two habitat types within a stretch of the Missouri River from Lewis and Clark Reservoir to Fort Randall Dam: the recreational river reach (upstream, distinct main channel, cold and clear water) and the delta section (downstream section with abundant side channels and backwater areas, water is warmer and more turbid than the recreational reach). During the spawning period (verified by egg collections), sauger were relocated only in the delta habitat where spawning occurred in secondary channels. Transmittered sauger apparently did not spawn in the riverine section, despite an abundance of gravel substrate. Sauger appeared to prefer spawning habitat with flowing water, warmer temperatures, and high physical turbidity. These patterns differ markedly from sauger spawning locations that were reported within 10 years of formation of this system by the closing of Gavins Point Dam.

Sauger historically spawned in the upper reaches of this system, near Fort Randall Dam. Sauger have apparently shifted spawning habitat preferences concomitant with the development of the novel delta habitat. The delta habitat likely functions more similarly to the historic Missouri River channel (increased temperature, turbidity, active meandering, complex habitats, etc.) as compared to the recreational reach, indicating that sauger prefer to spawn in areas with historic riverine function. Thus, future management activities intended to enhance sauger populations should focus on restoration of riverine function (e.g., habitat complexity, increased temperature, and increased turbidity), such as that provided by emerging reservoir deltas, that may mimic pre-impoundment conditions on the Missouri River.

Early studies of gizzard shad populations (during the first decade after reservoir formation) indicated that gizzard shad populations were at risk for extirpation because very few age-0 cohorts could survive winters and recruit to age 1. To determine the present status of gizzard shad recruitment and to assess gizzard shad reproduction I collected adult and larval gizzard shad from Lakes Sharpe and Francis Case. In contrast to earlier studies, and based on ages assigned to sagittal otoliths, gizzard shad recruitment was remarkably consistent, with no missing year classes and low variability in year-class strength. Originally, I had planned to model factors affecting recruitment following the same approach and methodology as *Sander* recruitment modeling, but because gizzard shad recruitment was consistent I had no variability to model. In fact, gizzard shad successfully recruited every year from 1992 to 2001, encompassing a range of environmental conditions (e.g., winter severity), and reservoir conditions (e.g., flood and

drought years), indicating that abiotic factors did not significantly affect recruitment of gizzard shad. Gizzard shad reproduction was concentrated in the upper two-thirds of each reservoir, and small (<20 mm total length) gizzard shad larvae were present in samples from June through early August, indicating a wide spawning window. Hipple Lake, a backwater in the upper section of Lake Sharpe was a particularly important site for gizzard shad reproduction with larval densities regularly exceeding 1,000 individuals/100 m^3 during peak hatching times in late June. The presence of small (<40 mm) gizzard shad throughout much of the summer suggests that they are widely available (i.e., wide range of sizes) for predators, including sauger for much of the growing season. Moreover, the consistent recruitment patterns of gizzard shad indicate that gizzard shad are have reduced risk of extirpation in these systems. Thus, gizzard shad are a desirable prey resource because they provide a stable and widely available prey resource for predators.

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List of Abbreviations

AIC.	Akaike's information criterion
AICc.	Akaike's information criterion corrected for small sample size
ΔAIC.	difference in AICc between each model and the most supported model
ALAT*.	alanine aminotranferase
BCS.	backcrossed sauger
BCW.	backcrossed walleye
C.	celcius
cms.	cubic meters per second
cm.	centimeter
d.	day
Disc.	discharge
F_1.	first generational hybrid
h.	hour
ha.	hectare
IDDH*.	L- iditol two-dehydrogenase
k.	number of model paramters
km.	kilometers
LCRS	Lewis and Clark reservoir system
m.	meter
m^3.	cubic meter

mm.	millimeter
μm.	micrometer
mMDH*.	Malate dehydrogenase
n.	sample size
p.	probability level
PGM-1*	phosphoglucomutase
r.	Pearson correlation coefficient
SE.	standard error
Spp	species
TEMP.	cumulative warming degree days
TRIB.	tributary
US.	United States
ACOE.	Army Corps of Engineers

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Chapter 1.

Introduction

Widespread declines in sauger *Sander canadensis* populations have been reported during the last several decades in the Missouri and Yellowstone rivers in Montana (McMahon and Gardner 2001), Great Lakes (Rawson and Schell 1978), Nebraska (Hesse 1994), Tennessee (Pegg et al. 1996), and Wyoming (Baxter and Simon 1970). These extensive declines have prompted researchers to classify sauger as a ’species of concern’ across portions of its range (McMahon and Gardner 2001). Furthermore, Hesse et al. (1993) recommended that sauger be listed as endangered in Nebraska. Loss of spawning habitat, climate conditions, changes in flow regimes, and introgression with walleye *Sander vitreus* are some factors suspected of contributing to declining sauger populations, but speculation is common due to a general lack of information. Although the specific mechanisms contributing to sauger declines are not well understood, deleterious effects from reservoir construction and climatological variation are common themes of many of these studies.

Reservoir management and climatological variation likely operate over multiple life stages to influence sauger population dynamics. Identifying the specific mechanisms influencing sauger recruitment is difficult because of complex life history. Adult sauger in large rivers utilize a variety of habitats on a seasonal basis, but habitat preferences often vary among populations (Pitlo 1992). Sauger generally migrate upstream to spawn during spring. In river-reservoir systems, spawning frequently takes place below reservoir tailraces because dams act as barriers (Siegwarth et al. 1993; Pegg et al. 1997), but can also occur at other locations within a pool (Pitlo 1992). Spawning success of adult sauger is likely influenced by availability of spawning habitat and environmental conditions during spawning (Nelson 1968; Pitlo 1992). Cobble and/or gravel substrate combined with stable water levels and temperatures during spawning and incubation apparently provide optimal conditions for sauger reproduction. Thus, a combination of abiotic factors may influence spawning success of adult sauger.

In addition to physical conditions present prior to and during spawning, the condition of female sauger during winter and early spring may affect nutritional quality of eggs produced, and subsequently survival of offspring. For example, the lipid content of female walleye (a close relative of sauger) in Lake Erie was positively correlated to recruitment success (Madenjian et al. 1996). Walleye in Lake Erie could only accumulate adequate lipid reserves when gizzard shad *Dorosoma cepedianum* were abundant during the fall prior to spawning. Although this specific relationship has never been examined for sauger in any system, gizzard shad are a primary prey species in lower Missouri River reservoirs (Johnson et al. 2002; Stone and Sorensen 2003; Wickstrom 2003), and have been shown to substantially increase growth of sauger in the Ohio River during fall (Wahl and Nielsen 1985). Thus, the availability of gizzard shad prior to spawning may influence sauger spawning success in Missouri River reservoirs.

After spawning, the survival of sauger eggs, larvae, and juveniles are also influenced by a suite of variables. Growth and survival during the first year of life can be particularly important because year-class strength is often determined during early life history in most fishes (Rice et al. 1987; Willis 1987). Sauger recruitment in the

Mississippi River was established during the first year of life (Lyons and Welke 1996), and I expect a similar occurrence in the Missouri River. Age-0 sauger may be particularly vulnerable to changes in habitat features such as water velocity, cover, and food availability mediated through reservoir operation. During the spawn, sauger eggs are typically deposited in relatively shallow water (e.g., <2.5 m in the Missouri River above Lewis and Clark Lake; Nelson 1968). Furthermore, because large variations in daily flow were common in this section of the Missouri River during the Nelson (1968) study (fluctuations of 1 m or more were typical below Fort Randall Dam), eggs deposited in shallower sites were exposed to air, resulting in complete reproductive failure. However, eggs deposited in depths at or below the minimum water elevation had high hatching success.

Little is known about larval sauger in rivers because of logistical constraints of sampling larvae (Pitlo 1992). Newly-hatched larval sauger are passively transported downstream, and sampling efforts to capture larvae in the water column are difficult because larvae can be found anywhere in a river section, and sampling gear is prone to fouling, which inhibits filtering sufficient water volume. As larvae grow and mature, they become demersal and occupy benthic habitats through adulthood. These juvenile (>30 mm) fish are susceptible to many sampling gears, and occupy more discrete habitats. Because of this complex early life history, sauger may be particularly at risk during the period from hatching until the late juvenile stage. If flows are high, larvae may be transported into areas of either higher predation or lower food availability, or in some cases, completely out of a system. For example, flushing rates of larval walleye and sauger through Gavins Point Dam were as high 700,000 fish per d (Walburg 1971). Flow rates may continue to affect sauger as juvenile fish if they become demersal in sub-optimal habitats.

Adult sauger commonly hybridize with walleye in some systems (Van Zee et al. 1996; Leary and Allendorf 1997; Billington 1998), potentially reducing fitness of offspring (Philipp et al. 2002). Natural hybridization with walleye in Lewis and Clark Lake (the furthest downstream Missouri River reservoir) was 10% (Van Zee et al. 1996), which was similar to another Missouri River reservoir, Lake Sakakawea, North Dakota (Ward 1992), but higher than for the farthest upstream reservoir, Fort Peck, Montana (6-9.5%; Billington 1998; Leary and Allendorf 1997). Natural hybridization rates in Lakes Francis Case and Sharpe have never been examined. Although factors influencing the extent of walleye introgression with sauger are poorly understood (McMahon and Gardner 2001), reduction of spawning habitat, possibly mediated by reservoir management, is thought to exacerbate hybridization (Nelson and Walburg 1977). Furthermore, age-specific recruitment models have not previously been constructed for hybrids. Thus, research is needed to determine if hybridization is patchy (i.e., large, inter-annual variation), and if hybridization rates are influenced by reservoir operation and climate.

Finally, the population biology of gizzard shad, a primary prey species in the lower three Missouri River reservoirs, is poorly understood in Missouri River reservoirs. South Dakota represents the northwestern limit of gizzard shad distribution (Pflieger 1975). As a result, gizzard shad likely experience substantial overwinter mortality

(White et al. 1986), and overly abundant adult populations are unlikely. Adult gizzard shad population characteristics were monitored by Walburg (1964) in Lewis and Clark Lake, by Gasaway (1970) in Lake Francis Case, and in Lake Sharpe by June (1987). All three authors reported that survival of juvenile gizzard shad to their second summer was very erratic because of winter mortality. Walburg (1964) reported no apparent overwinter survival of age-0 gizzard shad when reservoir ice cover exceeded 103 d. June (1987) found that the 1966 year class was the only group of adult gizzard shad collected from Lake Sharpe during 1967-1974 samples; age-0 shad were collected each year. Thus, first-winter mortality is likely a primary determinant of gizzard shad recruitment.

Sauger are an important component of the Missouri River fish assemblage as both a native predator and sportfish. While other sauger populations have shown marked declines in recent years (e.g., McMahon and Gardner 2001; Pegg et al. 1996), sauger populations in the lower Missouri River Reservoirs appear stable (e.g., Wickstrom 2003). However, the general ecology of sauger is poorly understood throughout their range, and potential effects of changes in reservoir water management for the Missouri River system are unknown. For example, if spring flows in the Missouri River are elevated above normally managed flows to simulate historical flooding, the potential changes in reproductive success of sauger (either positive or negative) are unknown. A broad-based recruitment assessment coupled with modeling procedures to identify important abiotic and biotic factors related to year-class strength is needed at this time. Specific mechanisms driving these relationships also need to be identified. Thus, I conducted a series of field research projects combined with modeling techniques to address the following questions.

1. What abiotic and biotic factors affect sauger year-class strength in Missouri River reservoirs?
2. What is the extent of hybridization between walleye and sauger in Missouri River reservoirs?
3. Is annual variation in hybridization influenced by climate and reservoir management?
4. What is the preferred spawning habitat of sauger in Missouri River systems?
5. Is gizzard shad recruitment annually erratic?
6. What abiotic factors affect gizzard shad year-class strength?

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Chapter 2.

Age Structured Assessment of Sauger, Walleye, and Naturally Produced Hybrids in Missouri River Reservoirs

Widespread declines in sauger *Sander canadensis* populations have been reported during the last several decades in the Great Lakes (Rawson and Schell 1978), the Missouri and Yellowstone rivers in Montana (McMahon and Gardner 2001; Jaeger et al. 2005), Nebraska (Hesse 1994), Tennessee (Pegg et al. 1996), and Wyoming (Baxter and Simon 1970). These extensive declines have prompted researchers to classify sauger as a ’species of concern’ across portions of its range (McMahon and Gardner 2001). Furthermore, Hesse et al. (1993) recommended that sauger be listed as endangered in Nebraska. Loss of spawning habitat, migration barriers, climate conditions, and genetic introgression with walleye *Sander vitreus* are common factors suspected of contributing to declining sauger populations in these locations.

While other sauger populations have shown marked declines in recent years, sauger populations in the three lower Missouri River reservoirs, Lewis and Clark, Francis Case, and Sharpe, have remained relatively stable (i.e., sauger populations have not declined; Lott et al. 2002; Sorensen 2003; Wickstrom 2004). These sauger populations remain stable despite experiencing several shortcomings identified in recent studies. For example, restoration of natural riverine function and removal of migration barriers have been proposed as conservation measures for sauger (Amadio et al. 2005; Jaeger et al. 2005); the three lower Missouri River reservoirs have migration barriers (dams), and additionally Sharpe and Francis Case have limited fluvial function (i.e., limited riverine habitat above each reservoir). In contrast, Lewis and Clark does maintain riverine habitat (70 km of riverine habitat above the reservoir), and is also likely expanding riverine function with the very large and continually growing delta at the upper end of the reservoir (Chapter 3). Despite these incongruencies, all three of these reservoirs maintain stable sauger populations. Further, because of the shared stability, yet physical differences, these three systems provide suitable locations to study factors influencing sauger populations.

My objectives were to quantify factors influencing sauger recruitment in these three Missouri River reservoir systems and to determine both the extent of hybridization between sauger and walleye and factors influencing recruitment of hybrids into the *Sander* spp. community. Recruitment assessments for sauger are limited, but I was able to utilize two comparative sauger recruitment studies, one from the Mississippi River (Pitlo 2002), and a study of sauger recruitment in Lewis and Clark shortly after formation of the system with the closure of Gavins Point Dam (Walburg 1972). These two studies guided *a priori* model formation and allowed me to compare the current study with sauger recruitment in another large river system, and to examine temporal changes in sauger recruitment associated with reservoir aging. I first developed an age-structured and genetically identified database of the sauger and walleye populations in these three systems. This database was then used to determine extent of hybridization, patterns of hybrid recruitment in these populations (synchrony with parental species), and finally to model abiotic factors (e.g., reservoir operation and climate) influencing recruitment of sauger, walleye, and hybrids. Understanding these processes is crucial to the current management of Missouri River reservoirs, as factors such as the influence of reservoir and flow management on native fishes, the role of hybridization, and designation of important habitat are not well understood. Further, reservoirs are a common feature of many river landscapes and understanding processes important to native fish recruitment in these systems has substantial implications for fish conservation in altered systems.

Methods

Study Area

I collected *Sander* spp. from the lowest three Missouri River reservoirs, Sharpe, Francis Case, and Lewis and Clark. A thorough characterization of these systems was compiled by Nelson and Walburg (1977); I summarize their findings below. Lake Sharpe (farthest upstream impoundment of the three) extends from Oahe Dam to Big Bend Dam in central South Dakota. Surface area for Lake Sharpe is approximately 25,000 ha, with maximum and mean depths of 23.7 m and 9.5 m. Lake Francis Case is immediately below Lake Sharpe, extending from Big Bend Dam to Fort Randall Dam. Francis Case is the largest of the three reservoirs at 32,000 ha; maximum and mean depths are 42.6 m and 15.2 m. Lewis and Clark Lake extends from Fort Randall Dam to Gavins Point Dam, borders both South Dakota and Nebraska, and is the smallest of the three reservoirs at 10,500 ha, with a maximum depth of only 16.7 m and mean depth of 5 m. The Lewis and Clark system is also unique in that it contains approximately 70 km of riverine habitat above the lake. Lewis and Clark Lake and Lake Sharpe primarily function as water control and hydropower reservoirs resulting in reduced average fluctuations in water level (1.1 m for Lewis and Clark, 0.6 m for Sharpe). Conversely, Lake Francis Case is also used for flood control and water levels annually fluctuate 6 – 14 m.

Population structure and recruitment patterns

All *Sander* specimens were collected during 2002 using variable mesh gill nets in conjunction with the South Dakota Department of Game, Fish and Parks (SDGFP) standardized sampling (see Lott at al. 2002; Sorensen 2003; Wickstrom 2004 for details). Liver and tissue samples and otoliths were removed from the majority of *Sander* spp. collected in each reservoir for genetic identification and age determination. Muscle and liver tissues were screened with four diagnostic loci: malate dehydrogenase (*mMDH**) and phosphoglucomutase (*PGM-1**) from muscle and alanine aminotransferase (*ALAT*)* and L-iditol 2-dehydrogenase (*IDDH**) from liver (Billington and Koigi 2004). Sagittal otoliths were aged in either whole view (for younger individuals), or cracked, sanded, and viewed in section (for individuals >age-3). All otoliths were aged by two readers and age discrepancies were re-examined until both readers and a third party came to consensus. Quantification of year-class strength followed the residual method proposed by Maceina (1997) and modified by Maceina (2003). Year-class strength was then compared among parental species and hybrids and across systems with correlation analysis to determine recruitment synchrony among species and systems.

Population model

Weaker and stronger year classes for walleye, sauger and natural hybrids were identified and related to biotic and abiotic variables. I used daily water temperature measured at the dam of each reservoir by the US Army Corps of Engineers to determine cumulative warming degree days (Temp). To calculate Temp, I summed the degree days above 10° C (average daily temperature – 10) during May and June of each year of analysis. I restricted this examination of temperature to May and June to represent conditions during the hatching, larval, and early juvenile period of *Sander* spp. (Walburg 1972). I also examined mainstem Missouri River discharge and local tributary inputs into each reservoir as potential factors influencing hybridization and recruitment. Tributary inputs (Trib) were estimated as the cumulative mean daily flow from one major tributary in each system. I used U.S. Geological Survey stream gauge data to quantify cumulative discharge of the Bad River (Sharpe), the White River (Francis Case) and the Niobrara River (Lewis and Clark). These tributaries represent the largest tributary stream for each system. Mean daily flow was summed during January to June to incorporate early snow thawing events, spring snow melt, and late spring/early summer rains that were thought to be important to system productivity during the larval and early juvenile stage of *Sander* spp. (Stone 1997). Finally, mean daily discharge through each dam was summed during January to June to determine cumulative discharge (Disc) through each system (US ACOE).

I constructed biologically meaningful combinations of these variables into competing models and fit each model with regression. Models were compared using Akaike's information criterion (AICc, corrected for small sample sizes; Burnham and

Anderson 1998). To determine the appropriate scale at which to apply my models, I examined recruitment synchrony among species and populations using Pearson's correlation. If recruitment was synchronous (i.e., highly correlated year classes) among all three systems and/or species then I applied my models to a pooled dataset. However, if recruitment operated independently in each system then I built system and/or species specific models. The same suite of *a priori* candidate models was used for each set of models.

Results

I examined >460 individuals of a broad range of sizes (132 mm to 761 mm total length) and ages (age 0 to age 12) from each of the three reservoirs. The proportion of hybrids was generally low in the two larger reservoirs, Lakes Sharpe and Francis Case (Table 1). However, hybridization rates were relatively high (>20% of all individuals screened) in Lewis and Clark. The pattern of hybridization was not equal among the potential hybrid types. There were relatively few F1 hybrids in any of the reservoirs, ranging from 0% of all hybrids in Lake Francis Case to 8% of all hybrids in Lewis and Clark Lake (Table 1). Similarly, the proportion of hybrids that were backcrossed to sauger was relatively moderate, ranging from 19% in Lewis and Clark Lake to 40% in Lake Francis Case. The majority of all hybrids were backcrossed to walleye ranging from 60% in Lake Francis Case to 72% in Lewis and Clark Lake.

Hybrid recruitment was not synchronous with sauger recruitment in Lewis and Clark Lake (n=11 year classes, r= 0.42, P=0.20; Table 2). However, hybrids were generally synchronous with walleye in Lewis and Clark (n=9 year classes, r=0.73, P=0.03; Figure 1). Sample sizes of hybrids were insufficient in Francis Case (n=20) and Sharpe (n=21) for recruitment synchrony comparisons with either parental species. Sauger recruitment was synchronous with walleye recruitment in Francis Case (n=6 year classes, r=0.88, P=0.02), but sauger were not synchronous with walleye in Lewis and Clark (n= 9 year classes, r=0.55, P=0.12) and Sharpe (n=9 year classes, r=0.53, P=0.14; Table 2) (Figure 2-1). Given these patterns of synchrony, I modeled recruitment variation at the localized and species-specific scale for Lewis and Clark Lake and Lake Sharpe. Lake Francis Case was excluded from recruitment modeling because there were few year classes of sauger present (n=6), with few individuals beyond the age-4 cohort. Hybrid recruitment was only modeled in Lewis and Clark due to insufficient sample sizes of hybrids for recruitment modeling in Francis Case and Sharpe.

Among the *a priori* models examined, hybrid recruitment appeared to be influenced by dissimilar factors than either parental species. The most supported hybrid recruitment model for Lewis and Clark was temperature during the early life history (Table 3). The second most supported model (discharge) also warrants strong consideration as the level of support was less than 1 AICc distance from the most supported model. The generally warmer years with lower flow of 1990-1994 and 1998-2001 correspond to moderate-to-strong year classes of hybrids, whereas the relatively colder years with high flow of 1995-1997 correspond with relatively moderate to weak year classes (Figure 2). All other single factor, additive, and interactive models were much less supported.

In contrast to hybrids in Lewis and Clark, recruitment of sauger and walleye was influenced by tributary input and tributary and temperature interaction (Table 3). Because the interactive model was strongly supported for both walleye and sauger (<2 AICc) and contained the variable (tributary) from the most supported model, I concluded that the best model was the interactive effects model. During 1990-1994, tributary inputs were relatively low and temperature during the early life history of these fishes was relatively warm, corresponding to moderate-to-stronger year classes (Figure 3). Conversely, the period 1995-1997 experienced the highest tributary inflows and coolest temperatures recorded during this study, resulting in relatively moderate to weak recruitment. The interaction is best illustrated during the most recent period sampled (1998-2001) wherein tributary inputs remained relatively high, but temperatures were also relatively warm corresponding to moderate to strong recruitment. During two of the years of this study, factors other than (or in addition to) tributary inputs and temperature may have been important. The 1994 and 1998 year classes were slightly weaker then predicted based on tributary flows and temperatures.

Sauger and walleye recruitment in Lake Sharpe were similarly affected by temperature during the early life history. Temperature alone was the most supported model for both predators in Lake Sharpe (Table 4). Further, all other sauger recruitment models were much less supported as they were >3 AICc distant from the temperature model. In general, warmer temperatures during spring and early summer resulted in stronger year classes for sauger and walleye in this impoundment (Figure 4).

Discussion

I evaluated factors influencing sauger population ecology and the potential role of natural hybridization of sauger with walleye in sauger conservation. Hybridization rates were generally low in Lakes Sharpe and Francis Case, but were unexpectedly high in Lewis and Clark Lake. The variability in size and operation of these systems, in addition to the similarities in factors influencing recruitment of both parental species, may explain the patterns observed.

Hybridization rates in Lewis and Clark Lake were much higher during my study than previously documented for this system. A pilot study conducted on Lewis and Clark during 1995 screened 50 fish and documented 10% hybridization (Van Zee et al. 1996). I am uncertain if my current study, which screened 465 individuals, resulted in a more accurate estimate of hybridization, or if hybridization rates have indeed more than doubled to the current level of 21% during the 7-year period of 1995-2002. However, given the conservation status of sauger and that Lewis and Clark is the only population examined where sauger were more abundant than walleye, I urge continued monitoring of hybridization in this system to determine if hybridization rates are increasing.

Sauger hybridization rates in other Missouri River basin populations are also much lower than Lewis and Clark, ranging from 0 % in Bighorn and Boysen reservoirs, Wyoming (Krueger and Hubert 1997) to 9.5% in Fort Peck Reservoir, Montana (Leary and Allendorf 1997). Although my study and previous studies were able to document the extent of hybridization, I am uncertain of the mechanism regulating hybridization. I found that sauger and walleye did spawn in similar habitats and during similar time periods in Lewis and Clark Lake (Chapter 3), but the specific mechanisms determining hybridization, and the direction of hybridization (favoring introgression with walleye over sauger) are unknown. Conversely, I am uncertain if sauger and walleye spawning habitats and timing overlap extensively in Lakes Francis Case and Sharpe, where hybridization rates are much lower than in Lewis and Clark. Despite differences in these systems in terms of the extent of hybridization, similar directions of hybridization were documented in all three populations. Introgressed walleye composed the majority of hybrids sampled in each system, with a smaller percentage of introgressed sauger and very few F1 hybrids in any system. Thus, identification of a specific mechanism will likely be applicable to all the populations examined.

Factors affecting recruitment of *Sander* spp. hybrids in Lewis and Clark Lake and parentals in both Lakes Sharpe and Lewis and Clark shared the common positive influence of warmer temperatures during *Sander* spp. early life history, but recruitment differed among sauger, walleye, and hybrids and among systems with regard to the effect of flow. Higher than average recruitment during years with warmer spring and early summer periods was also a common theme of previous studies of sympatric sauger and walleye populations (Nelson and Walburg 1977; Pitlo 2002). Temperature is likely a proximate factor that represents several other variables and identifying these variables was beyond the scope of this study. However, previous research has identified several factors (largely from walleye recruitment studies) associated with temperature that may operate in the systems I studied. For example, temperature may mediate egg maturation rate, growth rate of larvae and juveniles, food availability, and production of potential competitors (Koonce et al. 1977; Madenjian et al. 1996; Hansen et al. 1998).

In contrast to temperature, the influence of flow on recruitment varied among populations. Increased flow, either from mainstem cumulative discharge (hybrids) or tributary inputs (parentals), was negatively associated with year-class strength in my models for Lewis and Clark Lake, whereas tributary inputs and discharge were not well supported in models for sauger in Lake Sharpe (although tributary input warrants future consideration for walleye). I am uncertain why increased discharge would negatively affect hybrids, but not sauger or walleye in Lewis and Clark Lake. I speculate that either hybrids experience differential survival during high flow years, or that walleye and sauger are less likely to hybridize during high flow years. Future research on the reproductive ecology of sauger and walleye with respect to the mechanisms governing hybridization would greatly improve understanding of hybrid year class formation.

The effect of flow on recruitment of sauger and walleye in Lewis and Clark was confounded by an interaction with temperature. Tributary inputs negatively affected recruitment of sauger and walleye when water temperatures were reduced, but the effect of tributary input was negated during warmer years. The importance of tributary stream flow (and the lack of mainstem discharge) differs from an earlier study on sauger recruitment in Lewis and Clark. Walburg (1972) reported higher than average sauger recruitment during years when daily flow variation over the spawning ground and reservoir exchange rate (a measure of discharge through the system) were reduced. My results likely differ from Walburg (1972) because of habitat changes that occurred in the system between study periods. The Walburg (1972) study occurred within 14 years after formation of the reservoir, and since that time an expansive “delta” area has formed at the upper end of Lewis and Clark, as a depositional area for sediments transported by the Niobrara River (the largest tributary to this system and the source of my tributary modeling data). Concomitant with the development of this delta habitat, sauger shifted from spawning near the upper reaches of this system (11 km downstream of the Fort Randall dam; see Nelson [1968] for details) during the Walburg (1972) study to spawning 50-70 km below Fort Randall dam in the recently formed delta habitat during my study (see Chapter 3). Because tributary inputs from the Niobrara River influence temperature and turbidity of delta habitat during the sauger spawning period, the influence of tributary input was likely much greater during my study than observed by Walburg (1972). Conversely, the influence of discharge from the Missouri River was likely more pronounced during the Walburg (1972) study as compared to this study, as he reported that sauger spawned in relatively shallow water (<1m) near Fort Randall Dam that became exposed to air during discharge fluctuations (often exceeding 1 m daily). In contrast, sauger spawning presently occurs over deeper water (>1.5m) and much farther from the dam (where water level fluctuations are less pronounced; Chapter 3). As such, the effects of variable discharge were likely dampened in the delta spawning habitat resulting in the reduced effects of mainstem discharge in this study.

The lack of influence by flow, but a strong effect of temperature, on recruitment of sauger in Lake Sharpe is similar to sauger recruitment patterns in Pool 13 of the Mississippi River (Pitlo 2002). Increased warming rates during the spring were associated with higher recruitment of sauger and walleye in Pool 13, but recruitment was unrelated to discharge in this system (Pitlo 2002). The physical effects of discharge or tributary flow are likely dampened in Lake Sharpe as compared to Lewis and Clark Lake given the magnitude of volume differences between these systems. Lake Sharpe has greater than four times the volume of Lewis and Clark Lake (Nelson and Walburg 1977), and thus changes in elevation, temperature, turbidity, etc. are likely reduced in Sharpe as compared to Lewis and Clark.

The lack of sufficient year classes in Lake Francis Case (particularly >age 4) to model recruitment variation may result from exploitation, which also has been documented in the Tennessee River (Maceina et al. 1998). Walleye population size structure in Lake Francis Case was negatively affected by angler harvest during the late 1980's, prompting implementation of more restrictive angling regulations (Stone and Lott 2002). Because sauger and walleye are managed in combination and both species exhibited similar age structure, sauger exploitation likely is similar to that for walleye. Although the risk of overharvest is currently reduced as compared to the late 1980's when few individuals >age 2 were present, I recommend continued monitoring of sauger age structure in Francis Case. Any further truncation in age structure should trigger an assessment of the need for further regulation of harvest.

The sauger populations I examined represent some of the few remaining populations that have not exhibited widespread population declines. Although the level of hybridization in Lakes Francis Case and Sharpe were within the range observed for other populations, hybridization in Lewis and Clark Lake was much higher than previously observed and may be increasing. I urge that future research be directed at understanding the reproductive ecology of sauger and walleye with respect to hybridization. Sauger recruitment is influenced by temperature and/or the interaction of temperature and tributary flow. Although sauger populations appear to be stable in these systems, if sauger populations experience prolonged declines in the future, I recommend that alteration to flow and/or discharge that favor warmer water (e.g., installing variable depth outlet tubes) be considered as a conservation effort. In contrast to natural lakes, temperature manipulation may be possible in Missouri River reservoirs by discharging water from warmer surface waters of upstream reservoirs. This manipulation would have the largest effect at the upper end of each reservoir, but an ongoing larval fish study indicates that densities of larval *Sander* spp. are highest in the upper 1/3 of Francis Case and Sharpe (Graeb, unpublished data).

The importance of tributary streams (and the resultant delta habitat) to sauger recruitment on Lewis and Clark Lake illustrates the value of maintaining tributary stream inputs to reservoirs. The importance of delta habitats associated with tributaries may become important to Lakes Sharpe and Francis Case as well, as both of these systems currently have deltas forming at the mouths of tributaries. Although these deltas are not nearly as developed as the Lewis and Clark delta, they continue to expand and may provide spawning areas for sauger in these systems, either now or in the future.

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Table 2-1. Total number of *Sander* spp. and naturally produced hybrids as determined by genetic analysis and sampled from three Missouri River reservoirs. Hybrids were denoted as F1 (cross between parentals), BCS (backcrossed to sauger), and BCW (backcrossed to walleye).

				Hybrids			
Lake	Total number screened	Sauger	Walleye	Total	F1	BCS	BCW
Sharpe	482	104	357	21	2	4	15
Francis Case	507	175	312	20	0	8	12
Lewis and Clark	465	223	144	98	8	19	71

Table 2-2. Age structure of genetically identified sauger, walleye, and naturally produced hybrids from three Missouri River reservoirs. Values represent total number of fish collected in each age group.

Age	Sharpe			Lewis and Clark			Francis Case		
	Sauger	Walleye	Hybrids	Sauger	Walleye	Hybrids	Sauger	Walleye	Hybrids
1	0	47	0	98	61	42	32	76	0
2	44	89	7	56	27	24	53	85	5
3	19	91	3	10	10	7	18	61	3
4	23	77	9	17	11	8	7	19	0
5	4	16	1	10	4	1	2	8	3
6	1	2	0	5	3	2	0	3	0
7	0	10	1	0	0	1	1	0	0
8	7	16	0	0	1	2	0	0	0
9	5	1	0	1	2	2	0	0	0
10	0	2	0	2	0	0	0	0	0
11	0	4	0	1	0	1	0	0	0
12	0	0	0	1	0	0	0	0	0

Table 2-3. Rankings of *a priori* models based on level of support to explain variation in recruitment of sauger, walleye and natural hybrids between these two species in Lewis and Clark Lake, South Dakota. The number of parameters (main factors plus error and intercept) is designated as K, Δ AICc is the difference in AICc between each model and the most supported model, and AICc weight is the relative weight of evidence for each model. Ranks were designated by Δ AICc and AICc weights (smaller Δ AICc and larger values of AICc weights indicate highest support). Temp represents cumulative warming degree days (above 10°C) during March through June, Disc represents cumulative discharge (mainstem Missouri River), and Trib represents cumulative inflow from the Niobrara River (a large tributary of this system).

Species	Model	K	AICc	Δ AICc	AICc weight
Hybrids	Temp	3	0.51	0.00	0.46
	Disc	3	1.15	0.64	0.33
	Trib	3	3.35	2.83	0.11
	Temp, Trib	4	4.39	3.88	0.07
	Temp x Trib	3	5.74	5.22	0.03
	Temp, Trib, Disc	5	13.39	12.87	0.00
Sauger	Trib	3	5.83	0.00	0.36
	Temp x Trib	3	6.10	0.27	0.32
	Temp	3	7.55	1.72	0.16
	Disc	3	7.65	1.83	0.15
	Temp, Disc	4	12.75	6.92	0.11
	Temp, Trib, Disc	5	17.94	12.11	0
Walleye	Trib	3	5.22	0.00	0.48
	Temp x Trib	3	7.02	1.80	0.19
	Temp	3	7.29	2.07	0.17
	Disc	3	7.38	2.16	0.16
	Temp, Disc	4	16.44	11.22	0.00
	Temp, Trib, Disc	5	31.42	26.20	0.00

Table 2-4. Rankings of *a priori* models to explain variation in recruitment of sauger, walleye in Lake Sharpe, South Dakota. The number of parameters (main factors plus error and intercept) is designated as K, Δ AICc is the difference in AICc between each model and the most supported model, and AICc weight is the relative weight of evidence for each model. Ranks were designated by Δ AICc and AICc weights (smaller Δ AICc and larger values of AICc weights indicate highest support). Temp represents cumulative warming degree days (above 10°C) during March through June, Disc represents cumulative discharge (mainstem Missouri River), and Trib represents cumulative inflow from the Bad River (a large tributary of this system).

Species	Model	K	AICc	Δ AICc	AICc weight
Sauger	Temp	3	10.48	0.00	0.62
	Trib	3	13.63	3.15	0.13
	Disc	3	13.68	3.20	0.13
	Temp x Trib	3	14.00	3.53	0.11
	Temp, Disc	4	17.44	6.96	0.02
	Temp, Trib, Disc	5	36.09	25.62	0.00
Walleye	Temp	3	8.02	0.00	0.40
	Trib	3	9.59	1.56	0.18
	Temp x Trib	3	9.67	1.65	0.18
	Disc	3	9.69	1.67	0.18
	Temp, Trib, Disc	5	12.81	4.78	0.04
	Temp, Disc	4	13.91	5.88	0.02

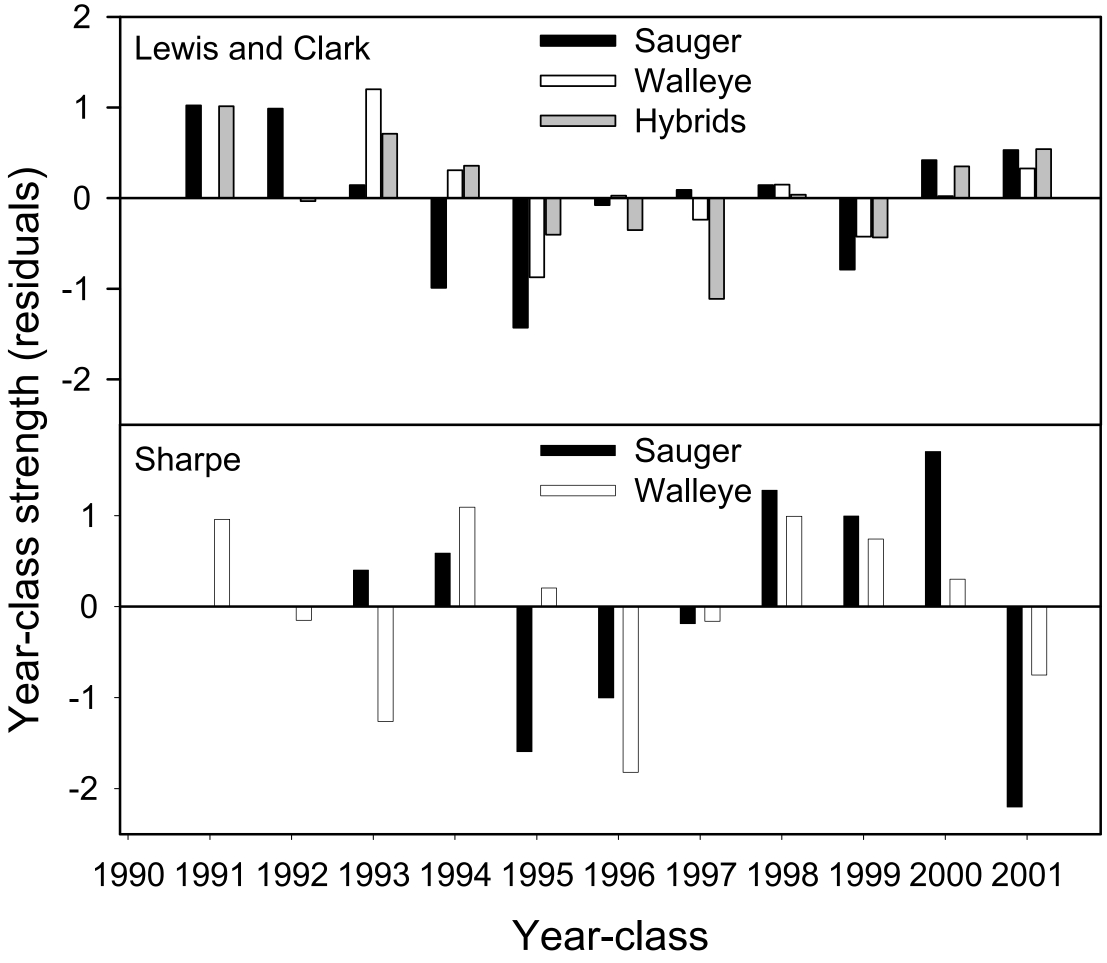

Figure 2-1. Year-class strength (as indexed by catch-curve residuals) of sauger, walleye, and naturally produced hybrids in Lakes Lewis and Clark and Sharpe during 1990-2001.

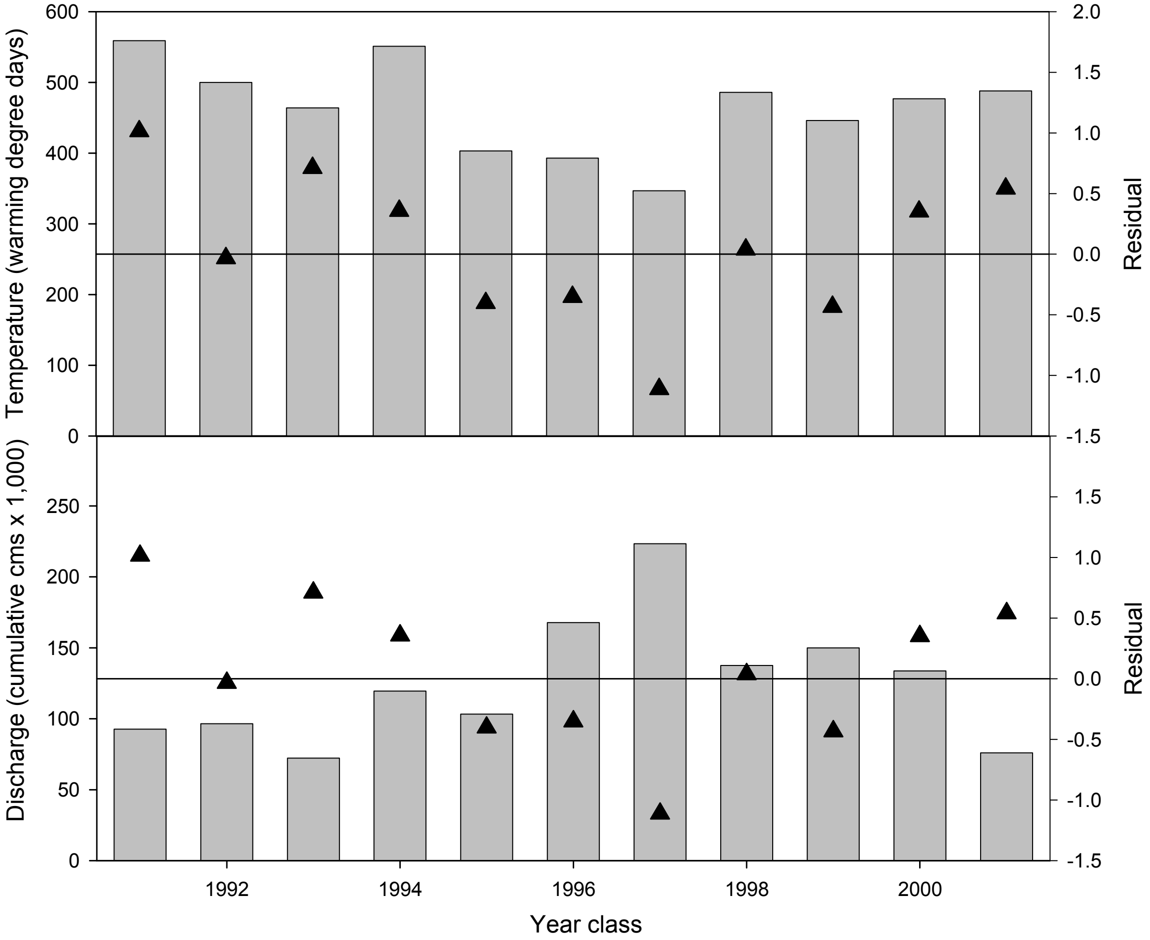

Figure 2-2. Temperature (cumulative warming degree days above 10°C from January-June, top panel) and mainstem Missouri River discharge (cumulative cms, bottom panel) and year-class strength of naturally produced hybrids (as indexed by catch-curve residuals; triangles) in Lewis and Clark Lake during 1990-2001.

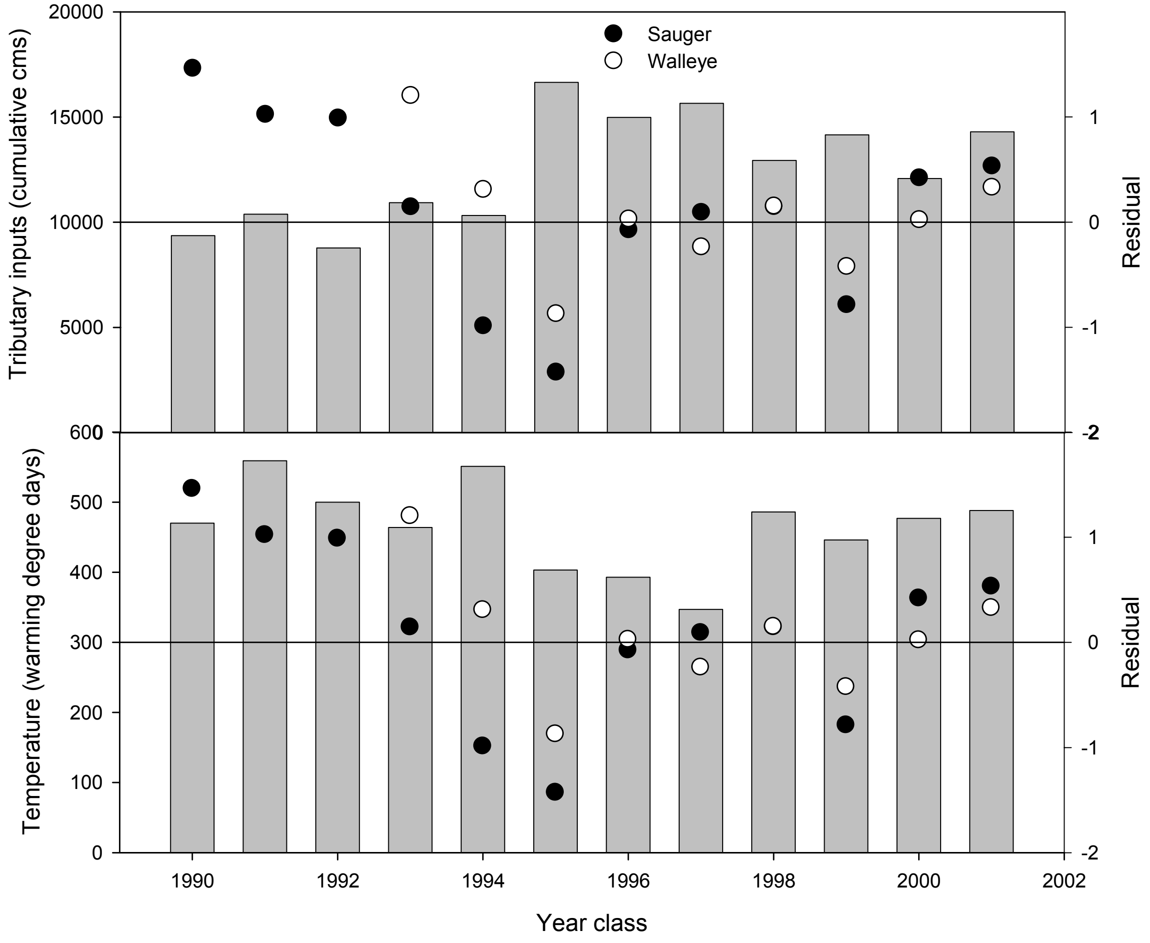

Figure 2-3. Temperature (cumulative warming degree days above 10°C from January-June, top panel) and mainstem Missouri River discharge (cumulative cms, bottom panel) and year-class strength of naturally produced hybrids (as indexed by catch-curve residuals; circles) in Lewis and Clark Lake during 1990-2001.

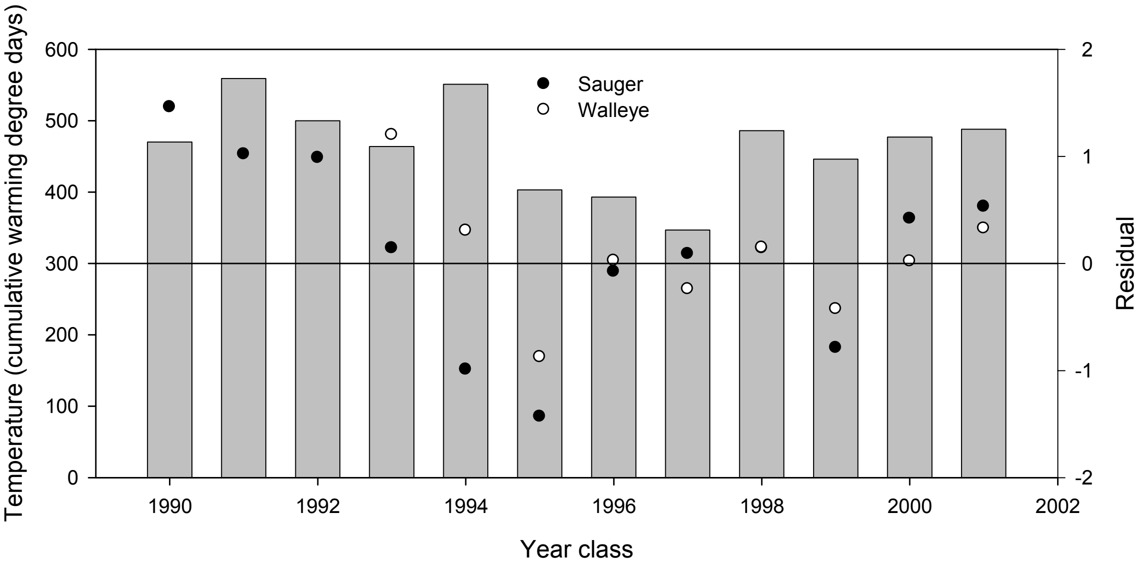

Figure 2-4. Temperature (cumulative warming degree days above 10°C from January-June) and year-class strength of sauger and walleye (as indexed by catch-curve residuals; circles) in Lake Sharpe during 1990-2001.

Chapter 3.

Shifts in sauger spawning habitats after 40 years of reservoir aging: influence of a novel delta ecosystem

Widespread declines in sauger populations have been reported during the last several decades in the Great Lakes (Rawson and Schell 1978), the Missouri and Yellowstone rivers in Montana (McMahon and Gardner 2001; Jaeger et al. 2005), the Missouri River in Nebraska (Hesse 1994), the Tennessee River (Pegg et al. 1997), and Wyoming streams (Baxter and Simon 1970). These extensive declines have prompted researchers to classify sauger as a ’species of concern’ across portions of its range (McMahon and Gardner 2001). Loss of spawning habitat either through river channel alteration (e.g., impoundments) or barriers to migration is a commonly identified factor in these studies contributing to declining sauger populations. In response to this common theme, researchers have called for restoration of natural riverine function and removal of migration barriers as conservation measures for sauger (Amadio et al. 2005; Jaeger et al. 2005)

While other sauger populations have shown marked declines in recent years, the sauger population in Lewis and Clark Lake (the lowest downstream Missouri River reservoir) has remained relatively stable (Wickstrom 2003) despite residing in an altered system (impoundment) with an upstream migration barrier (Fort Randall Dam). Lewis and Clark Lake maintains about 70 km of riverine habitat above the reservoir. A large and continually growing delta at the upper end of the reservoir, below the confluence with the Niobrara River, attests to the dynamic functions shaping habitat conditions in this system. The diversity of habitat available and the stable sauger population provide a unique opportunity to study sauger ecology.

In addition to a relatively stable sauger population, this system offers the opportunity to examine effects of reservoir aging on sauger spawning habitat across a long temporal scale. A sauger spawning habitat study conducted within 10 years of the formation of Lewis and Clark Lake (by closure of Gavins Point Dam in 1955; Nelson 1968) allowed me to assess how nearly 40 years of reservoir aging has affected the long-term changes in sauger spawning habitat in this system. Habitat changes most relevant to sauger spawning include changes to the riverine section above Lewis and Clark Lake. In contrast to the earlier study, potential sauger spawning habitat in the riverine section can now be separated into two functionally distinct sections, the delta and the recreational reach (so named because this reach was designated a National Recreational River by the National Park Service). My objective was to identify current sauger spawning habitat and to determine if sauger have shifted spawning site preference as the system has aged.

Methods

Study area

The Lewis and Clark reservoir system (LCRS; Figure 1) was formed in 1955 by the closing of Gavins Point Dam (Nelson 1968). The LCRS extends approximately 110 km from Fort Randall Dam to Gavins Point Dam and is the smallest (10,500 ha) and most downstream of the Missouri River mainstem reservoirs, with a maximum depth of only 16.7 m and mean depth of 5 m. It functions primarily as a water control reservoir resulting in low fluctuations in annual water level (mean = 1.1 m; Nelson and Walburg

1977). This system has developed into three distinct habitats over time: the reservoir, delta, and upstream riverine sections. Although sauger utilize all three habitats throughout the year, Nelson (1968) found that spawning occurred in the river during the first decade after dam closure.

The delta is a novel habitat that has been forming since closure of Gavins Point Dam, primarily from deposition of sediment transported by the Niobrara River, a large tributary stream of this system (Johnson 2002). The delta is a dynamic riverine habitat characterized as a braided channel with numerous backwaters, side channels, warmer temperatures, high turbidity, and connectivity to the floodplain. This habitat currently composes approximately 1/3 of the riverine reach (24 km out of 70 km) upstream from Lewis and Clark Lake, and is continually expanding downstream into the reservoir (Figure 1). In contrast, the recreational reach is characterized as a degrading channel with colder temperatures and clear water because of cold-water releases from Fort Randall Dam, and a loss of floodplain connectivity.

Telemetry

Adult sauger were collected immediately after ice-out in early March 2003 using electrofishing, gill netting, and angling. I spent 8 d collecting sauger from 14 locations throughout the entire study area (Fort Randall tailwaters to the upper end of Lewis and Clark Lake). Radio transmitters (Holohil Systems model PD-2, 90 d expected battery life) were externally attached to 50 mature sauger adults through the dorsal muscle behind the dorsal fin using Peterson type discs as stoppers. We tracked sauger weekly during spawning in April and approximately bi-weekly during postspawn through early June. The entire riverine section above Lewis and Clark Lake, as well as the upper 1/3 of the reservoir was monitored during tracking activities. We also monitored the Niobrara River to determine if sauger utilized this tributary stream for spawning. Global positioning system coordinates, water depth and temperature were determined from each of the suspected spawning sites.

Spawning activity was verified utilizing egg nets (20 x 50 cm rectangular opening, 50 cm deep, and 1,000 µm mesh; Pitlo 1989). These nets were fished overnight immediately below suspected spawning sites to collect eggs from spawning sauger. All eggs captured in nets were brought back to South Dakota State University and hatched so that larvae could be subsequently identified.

Results

I sampled for approximately 8 d during mid-March to early April and tagged a total of 50 sauger (n= 12 females and n=38 males). Sauger were initially tagged (n=15 total, 6 females and 9 males) from several locations throughout the delta and recreational reach, but the majority of fish (n=35 total, 6 females and 29 males) were captured from the confluence of the Niobrara River (Figure 1). Even though sampling was conducted throughout the study area (Fort Randall Dam to the upper end of Lewis and Clark Lake), sauger were only encountered from the powerline hole (approximately 20 km upstream from the Niobrara River confluence) to the upper end of Lewis and Clark Lake (Figure 1). Beginning the second week of April all tagged sauger moved into the delta and commenced spawning. We confirmed spawning activity by capturing and hatching eggs collected from one side channel in the delta where tagged sauger were always encountered (Figure 1). Sauger continued spawning for approximately 3 weeks as indicated by egg collections at this location.

Confirmation of sauger spawning via egg traps was unsuccessful at three other locations within the delta, but the side channel spawning site was similar to other habitats where sauger were located during the spawning period. The depth of this site ranged from 1 to 3 m, similar to where the majority of sauger were located during this period (Figure 2). The side channel was also similar to other habitats (off-channel habitats including side channels and backwaters) where sauger were frequently located during the spawning periods (Figure 3). During the spawning period and every post-spawn sampling period (through early June) sauger were always located in the delta habitat; transmittered sauger were never located in the recreational reach during the spawning or post-spawn period.

Discussion

Sauger spawning habitat locations in Lewis and Clark have shifted markedly after 40+ years of reservoir aging. All transmittered sauger in my study apparently avoided upstream areas of the recreational reach and instead focused activity during the spawning season in the delta. These changes are likely a result of the novel habitat that has developed as the system aged. The Missouri River channel has transformed into two distinct habitats since formation of the reservoir and sauger appear to prefer the delta habitat that retains riverine function most similar to the historic Missouri River channel. Availability of off-channel habitat, increased turbidity, and increased water temperatures are likely some of the factors resulting in sauger preferentially spawning in the delta as compared to the recreational reach. The Lewis and Clark delta continues to expand, which should further enhance sauger spawning habitat and could be an important feature related to the apparent stability of this sauger population.

A direct comparison between my study and Nelson's (1968) sauger spawning study is difficult because of general lack of habitat descriptions. He reported that sauger spawned primarily along rocky shorelines within 9 km of Fort Randall Dam, the upstream boundary of this system (Nelson 1968). I suspect that the Missouri River channel was relatively homogenous throughout this reach for the first several years after closure of Gavins Point Dam, which likely resulted in relatively similar habitat throughout much of the stretch, allowing sauger a wide range of available spawning habitat. Present habitat conditions in this stretch have been shaped for 40 years by the interacting forces of 1) predicted habitat changes downstream from reservoirs (serial discontinuity; i.e., sediment imbalance and associated degrading channel, cooler water temperatures, etc.; Ward and Stanford 1983), and 2) the influence of a large tributary stream (the Niobrara River) with a high sediment load creating the novel delta habitat (Johnson 2002). Rocky shorelines and/or areas with extensive gravel remain abundant in the recreational reach, but this stretch likely lacks other features important for sauger spawning. Specifically, the degrading channel in this stretch has decreased connectivity to the floodplain, reduced off-channel habitat, and is much colder and less turbid than historic conditions (National Research Council 2002). I documented sauger reproduction in an off-channel habitat within the delta, and this habitat was always warmer and more turbid than habitats within the recreational reach over the time period of this study. The delta habitat likely resembles conditions present in the recreational reach during Nelson's (1968) study (or at least at the time of dam closure) than present conditions. Thus, the shift in sauger spawning locations may simply be a result of the shift in availability of appropriate habitat as the system aged.

My results also suggest that sauger populations in other Missouri River reservoirs may similarly benefit from delta formations associated with reservoir aging. Development of the delta habitat in Lewis and Clark has occurred at a much faster rate than other systems because of the relatively small size of the reservoir in relation to the size of the Niobrara River watershed (Johnson 2002). However, similar habitats are developing in all of the other mainstem Missouri River reservoirs. For example, Lake Francis Case (the next system upstream from Lewis and Clark) currently has an expanding delta at the mouth of the White River, and Lake Sharpe has an expanding delta at the confluence with the Bad River. I predict that these areas could result in the expansion of suitable sauger spawning habitat.

My study compliments findings from recent studies on other Missouri River sauger populations. These studies, which were conducted on riverine populations (e.g., Amadio et al. 2005; Jaeger et al. 2005), recommended that restoration of riverine function and removal of migration barriers were necessary for sauger recovery. I contend that habitats with riverine function more similar to the historic Missouri River (i.e., deltas) are important, but that these habitats also can be found in reservoirs, and such habitat will likely expand as reservoirs age. Habitat within the delta includes multiple off-channel sites (side channels, secondary channels, etc.), the thalweg actively migrates across the floodplain, and the main channel remains connected to the floodplain. In fact, the delta habitat in Lewis and Clark is likely more similar to historic Missouri River riverine habitat than either the reservoir or the degraded recreational reach. Because deltas are relatively new landscape features they have yet to receive much attention from researchers in terms of ecosystem function (Johnson 2002), but given the importance of this habitat to one native Missouri River fish of concern, I urge further evaluation of the contribution of these novel habitats to the function of the Missouri River ecosystem.

While the sauger population in Lewis and Clark appears to have access to suitable spawning habitat, I caution that other factors may become important for sauger conservation in this system. For example, the potential deleterious effects of migration barriers are unknown at this time. Currently, sauger can be transported downstream as larvae via entrainment through Gavins Point Dam (Walburg 1971). Gavins Point Dam (and all other Missouri River reservoirs) lacks fish passage structure, which currently blocks the upstream dispersal of invasive Asian carps (Cyprinidae), but the long-term effects of sauger gene flow restrictions in the population are not certain. Furthermore, natural hybridization of sauger with walleye is higher in Lewis and Clark (22%) than any other documented Missouri River sauger population (Chapter 2). During this study I observed that ripe female and male walleyes overlapped temporally and spatially with spawning sauger. Future work on the interaction of sauger and walleye spawning in delta habitats would greatly improve our understanding of hybridization, as well as the role of delta habitat in structuring this interaction. However, from the perspective of sauger conservation, the directional nature of hybridization toward walleye (Chapter 2) seems a positive aspect because more walleye contained sauger genes than vice versa.

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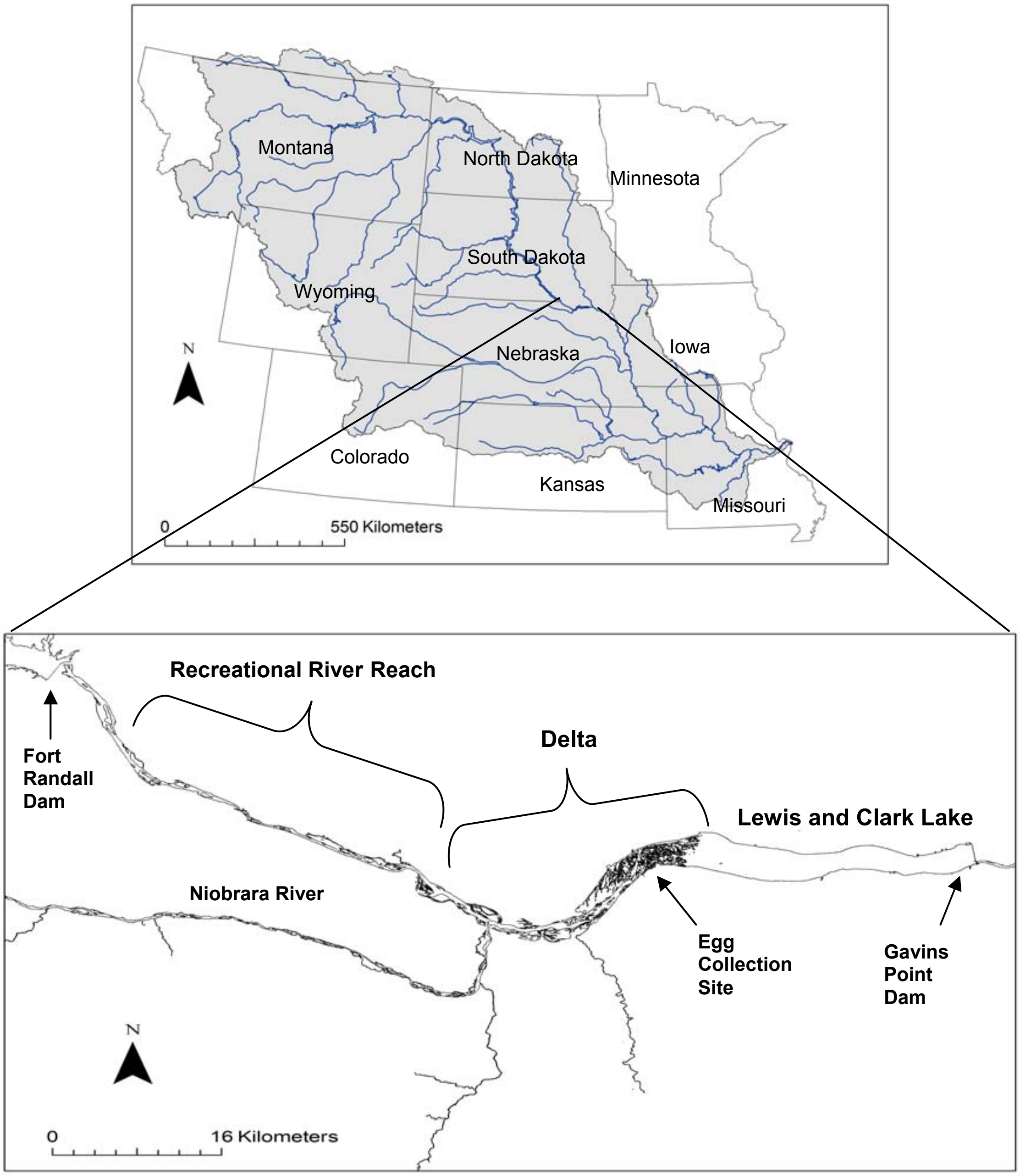

Figure 3-1. Missouri River watershed (top panel) and locations of study areas between Fort Randall Dam and Gavins Point Dam. The egg collection site is a side channel where I consistently collected sauger eggs during my study.

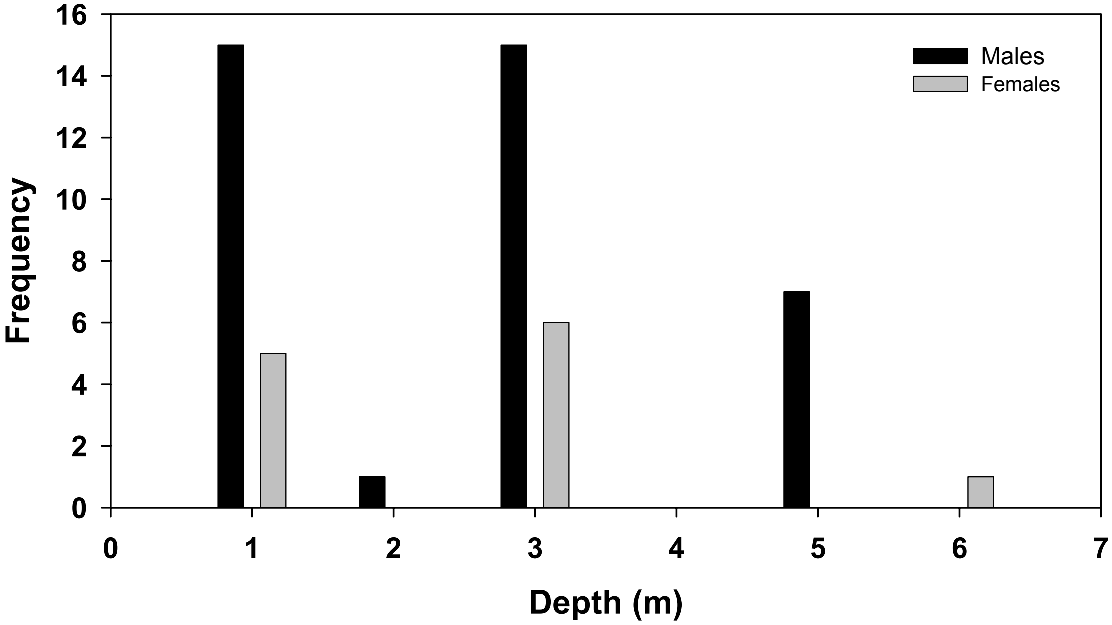

Figure 3-2. Frequency of depths occupied by sauger during the spawning season (April) as determined by radio telemetry in the Missouri River above Lewis and Clark Lake.

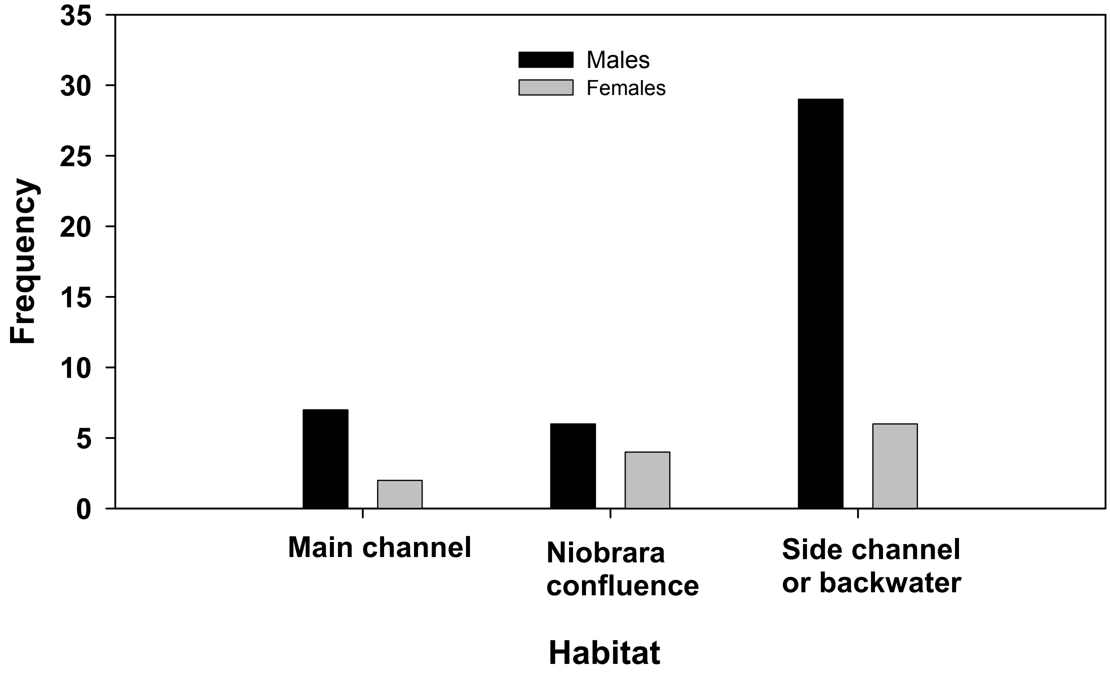

Figure 3-3. Frequency of habitats where sauger were relocated using radio telemetry during the spawning period (April) in the Missouri River above Lewis and Clark Lake.

Chapter 4.

Population Structure of Gizzard Shad in Three Missouri River Mainstem Reservoirs in South Dakota

South Dakota represents the northwestern limit of gizzard shad distribution (Pflieger 1975), primary prey species for *Sander* spp. in Missouri River reservoirs (Wickstrom 2006). Adult gizzard shad populations rarely become abundant in the upper Missouri River reservoirs, owing to overwinter mortality. As such, production of age-0 gizzard shad as a prey source for piscivores likely is more consistent than in southern populations because of reduced intraspecific competition (Willis 1987). Survival of juvenile gizzard shad to their second summer in Missouri River reservoirs apparently is erratic because of winter mortality. Walburg (1964) reported no apparent overwinter survival of age-0 gizzard shad in Lewis and Clark Lake in years when reservoir ice cover exceeded 103 d. June (1987) found that the 1966 cohort was the only group of adult gizzard shad collected from Lake Sharpe during 1967-1974 samples; age-0 shad were collected each year. In fact, because of the lack of recruitment in Lake Sharpe, June (1987) predicted that gizzard shad were at risk for extirpation in this system.

Based on prior work by Walburg (1964) and June (1987), I expected few year classes of adult gizzard shad to be present in the lower Missouri River reservoirs. Similar to the sauger recruitment assessment (Chapter 2), I planned to relate gizzard shad recruitment variability to environmental and reservoir operation variables. I predicted that winter severity was likely the most important factor influencing gizzard shad recruitment. The recruitment modeling assessment was dependent on 1) variability in recruitment patterns (i.e., missing and/or highly variable year classes), and 2) sufficient sample sizes (I assigned 100 adults as a minimum sample size). Concomitant with the recruitment assessment, I also collected larval gizzard shad in these systems to identify patterns of availability of gizzard shad prey in these systems.

Methods

Recruitment

I collected adult gizzard shad using daytime electrofishing during the spring spawning period of 2004 in Lakes Sharpe, Francis Case, and Lewis and Clark. Fish were measured to the nearest millimeter (total length), and sagittal otoliths (Clayton and Maceina 1999) were removed to determine the size and age structure of each gizzard shad population. Mean length at age by cohort was determined for female and male gizzard shad to assess potential growth differences among populations and between sexes.

Recruitment modeling followed the information-theoretic approach outlined in Chapter 2 and used Maceina's (1997) residual method (e.g., Maceina and Stimpert 1998) to provide an index of year-class strength. In addition to the variables utilized for sauger, walleye, and hybrid recruitment modeling (i.e., tributary inputs, discharge, and temperature during the growing season), I also included an index of winter severity (cumulative days when water temperatures were below 10° C from November to March). I planned to model all three systems separately if they met the *a priori* requirements for modeling (i.e., a population had to experience variable recruitment and I needed to be able to collect at least 100 adult gizzard shad).

Reproduction

Gizzard shad larvae were sampled during 2004 and 2005 in Lakes Sharpe and Francis Case, and during 2005 in Lewis and Clark Lake. I followed a stratified-random sampling design for Lakes Sharpe and Francis Case wherein each reservoir was divided into three approximately equal strata (upper, middle, and lower reservoir sections) from which six sites were randomly chosen during each sampling period. Additionally, Hipple Lake, a backwater lake in the upper section of Lake Sharpe that was suspected to be an important larval gizzard shad habitat, was sampled separately during each period. Lewis and Clark Lake was sampled at fixed sites to determine the larval fish contribution from the delta section upstream of the reservoir (see Chapter 3 for detailed description of the delta habitat). I sampled one site above the delta (Verdell), two sites in the delta (Springfield and Santee), two tributary streams of the delta (Bazille, and Niobrara), and two sites in Lewis and Clark Lake below the delta (upper and lower reservoir).

Sampling commenced in late April and early May of each year and occurred every two weeks until August (except for Lake Francis Case in 2004 when sampling ended in late June). Larval gizzard shad were collected with a 1-m diameter ichthyoplankton trawl with 1,000 µm mesh (bar measure) towed 10 m behind the boat for 10 min at all lake sites. Riverine sites were sampled by suspending the trawl in the current behind an anchored boat. The tributary sites were sampled by lowering a 0.5-m diameter trawl (same mesh size) over bridges that crossed each stream (Nebraska State Highway 12). A flowmeter was suspended inside the mouth of the trawls to determine the volume of water sampled and to estimate larval density (larvae/100 m^3). Samples were preserved in 90% ethanol and transported to the laboratory for identification and enumeration.

Results

Recruitment

I collected 126 adult gizzard shad (63 females and 61 males) from Lake Sharpe. All adult gizzard shad were collected from the Hipple Lake and Counselor Creek areas of Lake Sharpe during March and April. Gizzard shad adults were readily captured during this period in these two locations, likely because these waters were warmer than surrounding waters. Hipple Lake is a protected backwater lake in the upper portion of Lake Sharpe that generally warms more rapidly than surrounding water. Similarly, Counselor Creek is in the lower portion of Lake Sharpe (near Big Bend Dam), and adult gizzard shad were collected in the upper reaches of this embayment following a rain event with associated runoff that increased the turbidity and temperature of the embayment. Gizzard shad ranged in ages from 3 to 11 (Figure 1) and were 281 - 481 mm (Figures 2). Growth rates of males and females were relatively similar from age 3 to age 8 (Figure 3). Older females were underrepresented in our samples. If this sample accurately represents the proportion of older gizzard shad females, then there is potential for differential mortality between males and females beyond age 8, with only slower growing females surviving to these older ages. Recruitment of gizzard shad in Lake Sharpe was remarkably consistent (Figure 1). There were no missing year classes and inter-annual variability was very low. Because of the consistent recruitment of gizzard shad (little annual variability) in Lake Sharpe, I did not model the effects of climatological and reservoir operation variables on recruitment. In fact, it is important to note that gizzard shad recruitment remained consistent across 11 years of variable conditions, including high water years (late 1990's), low water years (early 2000's), and winters with varying degrees of severity.

In contrast to Lake Sharpe, I only collected 59 adult gizzard shad (47 females and 12 males) from Lake Francis Case. Approximately half of the gizzard shad collected (n=29) came from one sampling event (electrofishing) conducted at the American Creek embayment in the town of Chamberlain during March. This location has a large artesian well that maintains warmer temperatures in the embayment during winter and early spring than surrounding waters, and likely serves as overwinter habitat for gizzard shad. Thus, gizzard shad appeared to be easily collected from this site just after ice-out. To increase the sample size of adult gizzard shad, I further sampled Lake Francis Case during May, but I experienced unexpectedly low catch rates. I electrofished approximately 10 d (with approximately 4-5 h of active electrofishing/d) during May in several areas of Lake Francis Case and captured only 30 additional adult gizzard shad. The majority of these adults were captured in the Snake Creek and Pease Creek embayments (approximately mid-reservoir). Additional sampling at American Creek, tailwaters of Big Bend Dam, and several embayments throughout the lake resulted in no further captures. The most consistent catches during May (Pease Creek and Snake Creek) occurred in the upper ends of large embayments with flowing tributary streams. I collected adult gizzard shad from age 3 to age 7 that ranged in total length from 354 mm to 563 mm (Figures 1 and 2). Growth rates were relatively consistent between males and females across all ages (Figure 3), but gizzard shad attained larger sizes in Lake Francis Case than Lake Sharpe (Figures 2 and 3). Recruitment also was relatively consistent in Lake Francis Case (no missing year classes), but there was variability among year classes. However, because of the reduced sample size (less than 100 individuals) I did not attempt to model this variability as a function of climate or reservoir operation. Despite the annual variability, it is important to note that there were no missing year classes in our sample, indicating that at least some recruitment to the adult population occurred every year.

I conducted approximately 10 d of sampling (electrofishing and gill netting) to collect adult gizzard shad in Lewis and Clark Lake during May. I sampled embayments, shallow flats in the upper reservoir, and many areas in the delta habitat upstream of the reservoir and collected a total of nine adult gizzard shad. Similarly, during three years of intensive sampling (electrofishing and gill netting) for other projects in this system I have only collected one other adult gizzard shad (early April, Niobrara River mouth). Although I am confident that this system does support at least a limited adult population (see larval sampling results below), I am uncertain where to collect adults. Because of the low sample size I did not include Lewis and Clark Lake in gizzard shad population analyses.

Reproduction

Peak larval gizzard shad densities occurred in mid- to late June in all three systems and for both 2004 and 2005 in Lakes Sharpe and Francis Case (Table 1). Catches were generally higher and more consistent in the upper third of Sharpe and Francis Case, but variability was high, and precision was low throughout the study. In contrast to the main reservoir sites, larval gizzard shad were consistently collected from Hipple Lake on Lake Sharpe. Gizzard shad densities in this backwater lake were much greater than any other reservoir location, with a peak of >50,000 larvae/100 m^3 collected in June 2005, as compared to peak of 90 larvae/100m^3 during June 2004 for Lake Francis Case, 98 larvae/100 m^3 during June 2005 for all other samples in Lake Sharpe, and 584 larvae/100 m^3 during June 2005 in Lewis and Clark Lake. Larval gizzard shad were collected beginning in late May and early June during both years, and were present during all sampling periods through early August.

Larval gizzard shad in Lewis and Clark Lake were collected primarily in the reservoir, with only one sample (Niobrara River, early June) outside of the reservoir containing larvae (n=2). Gizzard shad densities within the reservoir were inconsistent between the upper and lower zones (i.e., neither zone was consistently higher than the other), but the peak abundance came from the lower zone during late June 2005 (584 larvae/100 m^3; Table 1). Larval gizzard shad were collected from early June to early August in Lewis and Clark Lake.

Discussion

Gizzard shad recruitment in Missouri River reservoirs was more consistent than I predicted based on previous research and recent studies of gizzard shad in another South Dakota system. In contrast to previous studies conducted on gizzard shad populations in Lake Sharpe during 1966 to 1974 when very few potential age groups were present (one year out of nine) in the population (June 1987), and a recent study in Angostura Reservoir, South Dakota, where only three out of 10 year classes were present (Ward et al. 2006), my shad population samples from Lakes Sharpe and Francis Case had no missing year classes and inter-annual recruitment variability was low. Moreover, given the current recruitment patterns of the Lakes Sharpe and Francis Case gizzard shad populations, shad obviously appear to be no longer at risk for extirpation. Previous researchers believed that gizzard shad recruitment at the northern edge of their range was erratic due to relatively low overwinter survival of age-0 gizzard shad (i.e., during most years, overwinter mortality was near 100%). Recent gizzard shad cohorts in Sharpe and Francis Case do not appear to be influenced by winter severity, as year classes have formed every year from 1993 to 2001 (encompassing a range of severe to moderate winters). Although gizzard shad have recruited during a range of winter conditions, I am uncertain as to the actual mechanism that allowed age-0 gizzard shad to survive winters during my study, and which apparently was absent or insufficient to allow consistent recruitment during the 1960's and 1970's. One potential explanation is that submerged artesian wells which are common in the Missouri River Valley (Davis et al. 1961) provide thermal refuge for overwintering age-0 gizzard shad. In fact, adult gizzard shad were readily collected at ice-out in the American Creek embayment (in the town of Chamberlain) on Francis Case. This embayment has a very large and readily identified artesian well that likely provided thermal refuge to overwintering gizzard shad. Future work monitoring the use of these habitats by gizzard shad and other fishes would improve our understanding of the winter ecology of fishes in these systems.

The low sample size of adult gizzard shad collected from Lewis and Clark despite the large amount of effort over 3 years of sampling, combined with the abundance of larval gizzard shad, poses potential future research questions. Specifically, while the presence of a low density adult population seems likely based on larval gizzard shad sampled, I am uncertain of the adult size and age structures, as well as the best habitats in which to collect them. I sampled shallow water (<2 m) areas of the reservoir and delta with limited success. Other locations not sampled include deep water habitat in the reservoir, the recreational reach above the delta (see Chapter 3 for description), and the Niobrara River. Evidence from larval sampling indicates that the number of larval fish produced in or above the delta likely was minimal as I collected no larval gizzard shad from the delta sites or the Verdel site above the delta. However, I did collect two larval gizzard shad from the Niobrara River during June 2005, indicating that at least some reproduction occurs in the Niobrara River drainage. Although I only collected two gizzard shad from this site during the course of my study, this represents a potentially important finding as sampling efficiency was limited at this site because the shallow channel and high sediment load reduced the amount of water volume sampled as compared to other sites. Future research should examine the potential use of this tributary by gizzard shad.

The presence of larval gizzard shad in Lewis and Clark Lake is not likely a result of entrainment from Fort Randall Dam. In contrast to other Missouri River reservoirs such as Lewis and Clark (Gavins Point Dam), and Sharpe (Big Bend Dam), which draw water from relatively shallow areas (3-6 m) with documented potential for large biomass of larval fish entrainment [e.g., 700,000 fish/d through Gavins Point Dam (Walburg 1971) and 470,000 larvae/d through Big Bend Dam (Smith and Brown 2002)], Fort Randall dam has deeper outlet tubes (40 m) and entrainment is very low (Walburg 1971). Entrainment through the deep outlet tubes (40 m) at Garrison Dam (an impoundment of the Missouri River which forms Lake Sakakwea in North Dakota) similarly is very low (Wolf et al. 1996). Moreover, I did not collect any gizzard shad larvae at any of my mainstem larval sampling sites above the reservoir, suggesting that larvae are not drifting into the reservoir from upstream areas or from Fort Randall Dam. Thus, evidence from my study and previous studies suggests that gizzard shad are either spawning in the reservoir (and are difficult to collect as adults) or they are running up in the Niobrara River to spawn (and are difficult to collect as larvae).

Gizzard shad reproduction was concentrated in the upper and middle zones of Lakes Sharpe and Francis Case as larvae were more abundant in these areas. In Lake Sharpe, Hipple Lake is likely a very important area for gizzard shad reproduction. This site consistently had densities of larval gizzard shad far higher than any other sampling site or system. In fact, the peak densities observed (>50,000 larval gizzard shad per 100

m^3) exceeded peak abundances from other South Dakota reservoirs (Angostura, Shadehill, and Orman reservoirs all produced <1,000 individuals per 100m^3; Ward 2005). Furthermore, larval gizzard shad densities in Hipple Lake far surpass density estimates from many other systems (140 to >1,000 individuals per 100m^3; reservoirs in Arkansas, Oklahoma, Missouri, Lake Erie; summarized by Ward 2005). Given the consistently high densities of gizzard shad in Hipple Lake, and relatively low densities elsewhere in Sharpe, this site may serve as an important source of gizzard shad for the entire system.

My study represents the first comprehensive evaluation of gizzard shad recruitment and reproduction in Missouri River reservoirs since the 1970's. Substantial changes have occurred in these systems such that gizzard shad recruitment is now remarkably consistent in Sharpe and Francis Case. Moreover, the wide hatching window, as evidenced by the small (<20 mm) larvae that were present from June to August, ensures that a wide size range of gizzard shad is available to predators in these systems. Thus, gizzard shad appear to be an appropriate prey item for sauger and other piscivores in these systems, and recruitment patterns of these shad populations indicate that they are no longer at risk for extirpation.

This study also generated several questions that should be addressed by future researchers. The mechanism(s) allowing consistent recruitment are unclear, but given the importance of overwinter mortality future researchers should examine factors influencing overwinter survival of age-0 gizzard shad. The size structure, recruitment patterns, growth, and spawning habitat of adult gizzard shad in Lewis and Clark Lake should be quantified. Future work should focus on deepwater habitats and/or the Niobrara River as locations to collect adult gizzard shad. The importance of Hipple Lake as spawning habitat for gizzard shad in Lake Sharpe is highly evident in my study. In fact, given the extremely high densities of larvae in this area, it may be an important source of larval gizzard shad for all of Lake Sharpe.

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Table 4-1. Mean density (number per 100 m^3 ± SE) of larval gizzard shad collected from various sites in Lakes Sharpe, Francis Case, and Lewis and Clark during 2004 and 2005. Six replicate tows were conducted at each site in Lakes Sharpe and Francis Case, except that a single tow was conducted at the Hipple Lake site (Lake Sharpe). One tow was conducted at each site in Lewis and Clark Lake.

Reservoir	Year	Date	Site	Gizzard shad (100 m^3)	SE
Sharpe	2004	11 May	Lower	0.09	0.06
			Middle	0.00	0.00
			Upper	0.00	0.00
			Hipple	0.00	0.00
		26 May	Lower	0.55	0.35
			Middle	0.00	0.00
			Upper	0.00	0.00
			Hipple	106.83	.
		1 June	Lower	0.04	0.04
			Middle	0.00	0.00
			Upper	0.04	0.04
			Hipple	784.54	.
		7 June	Lower	0.10	0.06
			Middle	0.39	0.33
			Upper	0.09	0.06
			Hipple	1848.4	.
		14 June	Lower	0.33	0.27
			Middle	0.05	0.05
			Upper	5.04	3.08
			Hipple	2066.51	.
		22 June	Lower	10.35	9.58
			Middle	3.69	2.38
			Upper	4.79	2.86
			Hipple	3766.51	.
		20 July	Lower	2.03	0.56
			Middle	1.50	1.33
			Upper	3.07	3.07
			Hipple	366.38	.
		9 August	Lower	0.00	0.00
			Middle	0.42	0.42
			Upper	7.18	4.59
			Hipple	302.91	.
	2005	16 May	Lower	0.00	0.00
			Middle	0.00	0.00
			Upper	0.00	0.00

Table 1 Continued.

Reservoir	Year	Date	Site	Gizzard shad (100 m^3)	SE
Sharpe	2005	16 May	Hipple	0.00	0.00
		31 May	Lower	0.09	0.09
			Middle	29.55	16.68
			Upper	2.10	1.20
			Hipple	5082.28	0.00
		14 June	Lower	18.07	11.63
			Middle	4.31	1.15
			Upper	18.21	13.21
			Hipple	50143.11	.
		27 June	Lower	0.54	0.46
			Middle	98.29	70.79
			Upper	28.45	10.80
			Hipple	1300.03	.
		11 July	Lower	8.44	7.65
			Middle	60.32	27.22
			Upper	2.80	2.21
			Hipple	48.92	.
		25 July	Lower	0.19	0.19
			Middle	3.98	2.23
			Upper	13.56	4.86
			Hipple	34.03	.
		8 August	Lower	2.34	0.78
			Middle	2.40	0.39
			Upper	0.30	0.20
			Hipple	0.52	.
Francis Case	2004	10 May	Lower	0	0
			Middle	.	.
			Upper	.	.
		17 May	Lower	0.15	0.11
			Middle	0.20	0.20
			Upper	0.04	0.04
		14 June	Lower	0.40	0.40
			Middle	9.22	5.47
			Upper	52.49	26.47
		21 June	Lower	1.05	0.67
			Middle	5.73	4.99
			Upper	90.26	70.22
	2005	4 May	Lower	.	.

Table 1 Continued.

Reservoir	Year	Date	Site	Gizzard shad (100 m^3)	SE
Francis Case	2005	4 May	Middle	.	.
			Upper	0.00	0.00
		10 May	Lower	.	.
			Middle	.	.
			Upper	0.00	0.00
		19 May	Lower	0.00	0.00
			Middle	0.00	0.00
			Upper	0.00	0.00
		31 May	Lower	0.15	0.10
			Middle	0.34	0.19
			Upper	2.69	1.22
		5 June	Lower	2.35	1.09
			Middle	13.68	5.61
			Upper	44.58	40.82
		29 June	Lower	0.00	0.00
			Middle	6.06	3.35
			Upper	3.58	1.30
		11 July	Lower	0.00	0.00
			Middle	1.80	1.21
			Upper	5.96	2.97
		28 July	Lower	0.10	0.06
			Middle	0.00	0.00
			Upper	0.96	0.56
		8 August	Lower	0.00	0.00
			Middle	0.00	0.00
			Upper	0.00	0.00
Lewis and Clark	2005	28 April	Bazille	0.00	.
			Lower lake	0.00	.
			Niobrara	0.00	.
			Upper lake	0.00	.
			Santee	0.00	.
			Springfield	0.00	.
			Verdel	0.00	.
		13 May	Bazille	0.00	.
			Lower lake	0.00	.
			Niobrara	0.00	.
			Upper lake	0.00	.
			Santee	0.00	.

Table 1 Continued.

Reservoir	Year	Date	Site	Gizzard shad (100 m^3)	SE
Lewis and Clark	2005	13 May	Springfield	0.00	.
			Verdel	0.00	.
		25 May	Bazille	0.00	.
			Lower lake	0.00	.
			Niobrara	0.00	.
			Upper lake	0.00	.
			Santee	0.00	.
			Springfield	0.00	.
			Verdel	0.00	.
		9 June	Bazille	0.00	.
			Lower lake	28.65	.
			Niobrara	>0.00	.
			Upper lake	178.85	.
			Santee	0.00	.
			Springfield	0.00	.
			Verdel	0.00	.
		22 June	Bazille	.	.
			Lower lake	583.96	.
			Niobrara	0.00	
			Upper lake	110.13	.
			Santee	0.00	.
			Springfield	0.00	.
			Verdel	0.00	.
		7 July	Bazille	0.00	.
			Lower lake	4.4	.
			Niobrara	0.00	.
			Upper lake	0.94	.
			Santee	0.00	.
			Springfield	0.00	.
			Verdel	0.00	.
		22 July	Bazille	.	.
			Lower lake	6.48	.
			Niobrara	0.00	.
			Upper lake	3.23	.
			Santee	0.00	.
			Springfield	0.00	.
			Verdel	0.00	.
		1 August	Bazille	0.00	.
			Lower lake	0.81	.

Table 1 Continued.

Reservoir	Year	Date	Site	Gizzard shad (100 m^3)	SE
Lewis and Clark	2005	1 August	Niobrara	0.00	.
			Upper lake	3.33	.
			Santee	0.00	.
			Springfield	0.00	.
			Verdel	0.00	.

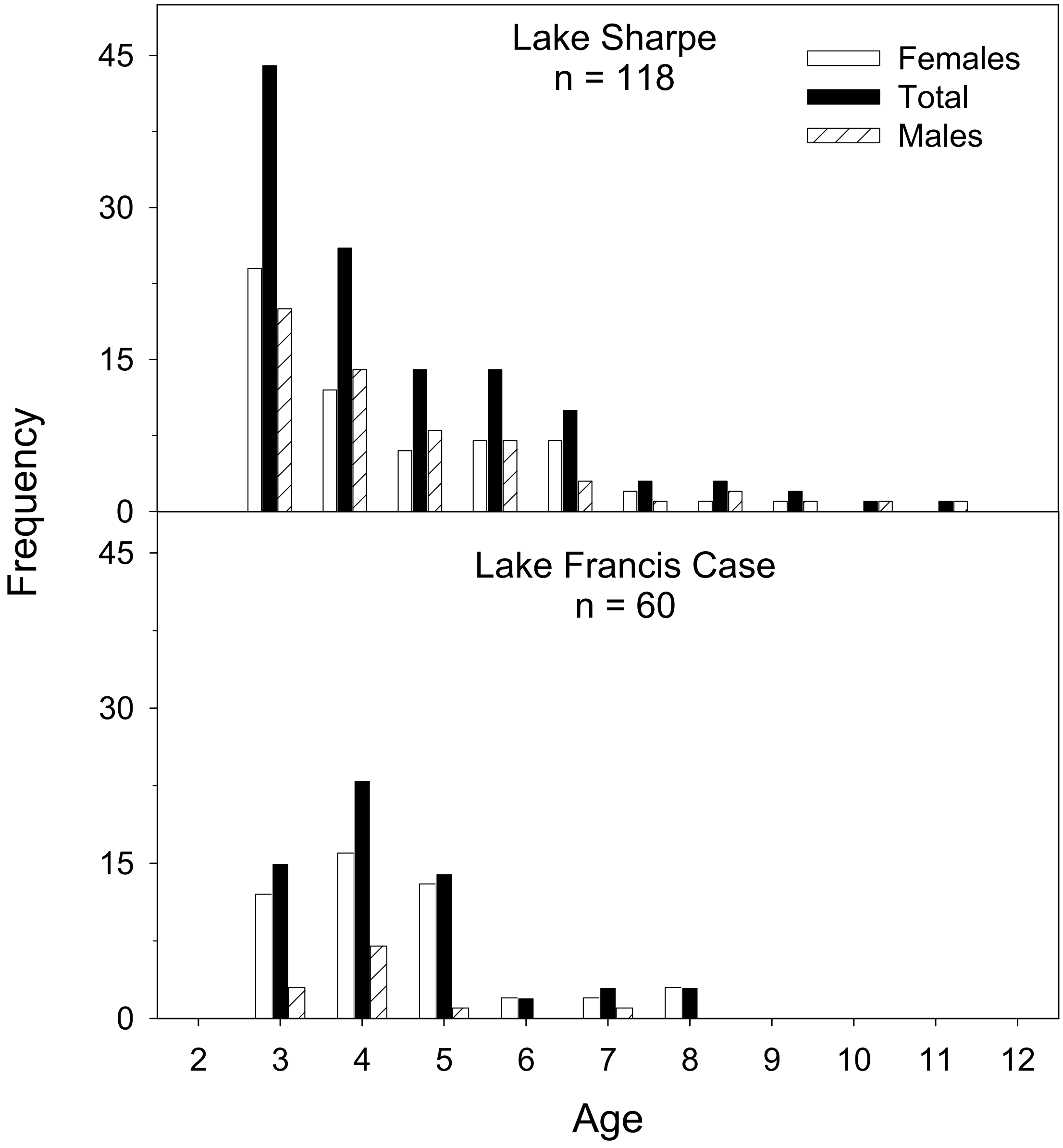

Figure 4-1. Age frequency distribution (determined from sagittal otoliths) of adult gizzard shad collected from Lake Sharpe and Francis Case during 2004.

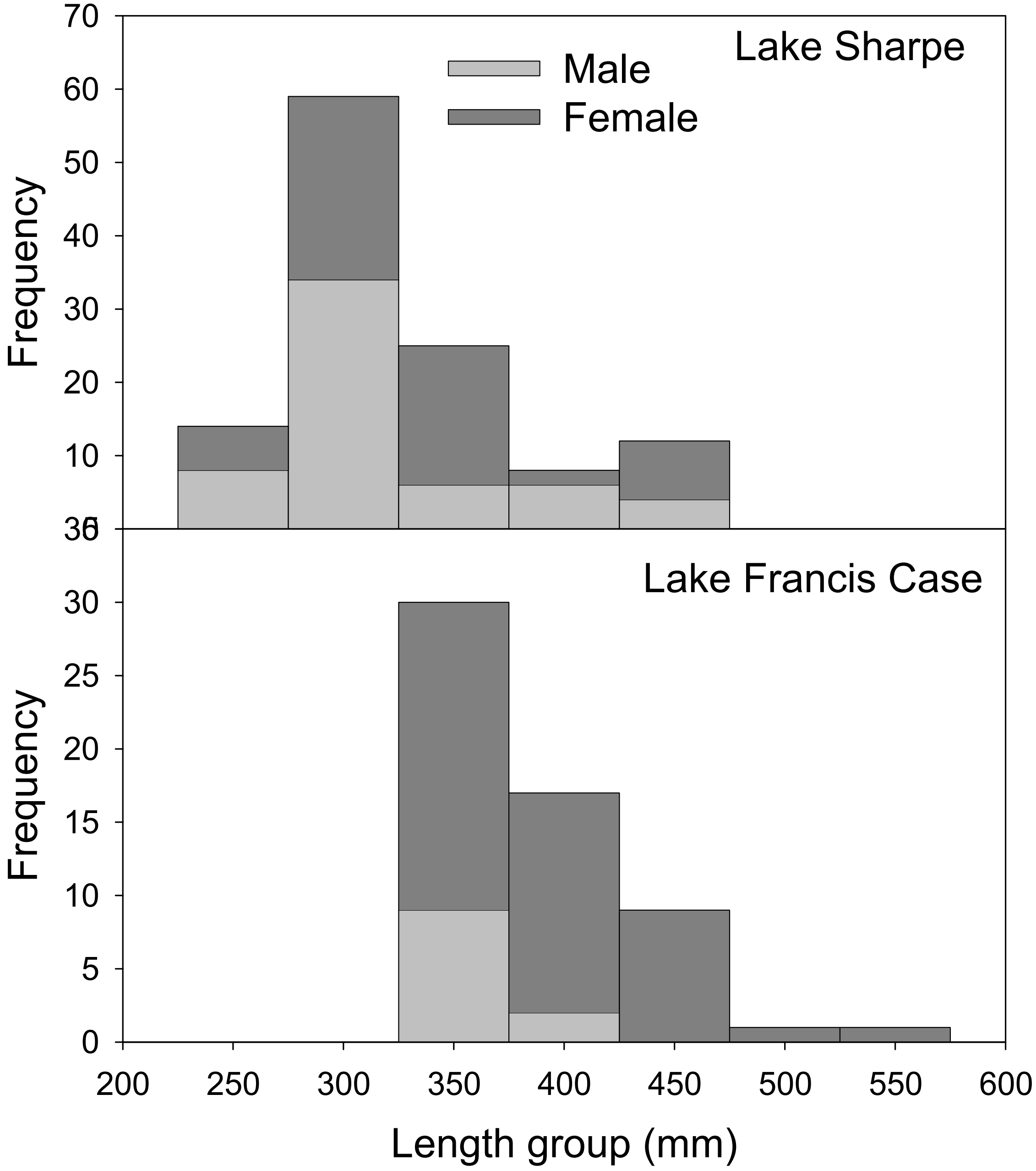

Figure 4-2. Length-frequency distribution of adult gizzard shad collected from Lakes Sharpe and Francis Case during 2004.

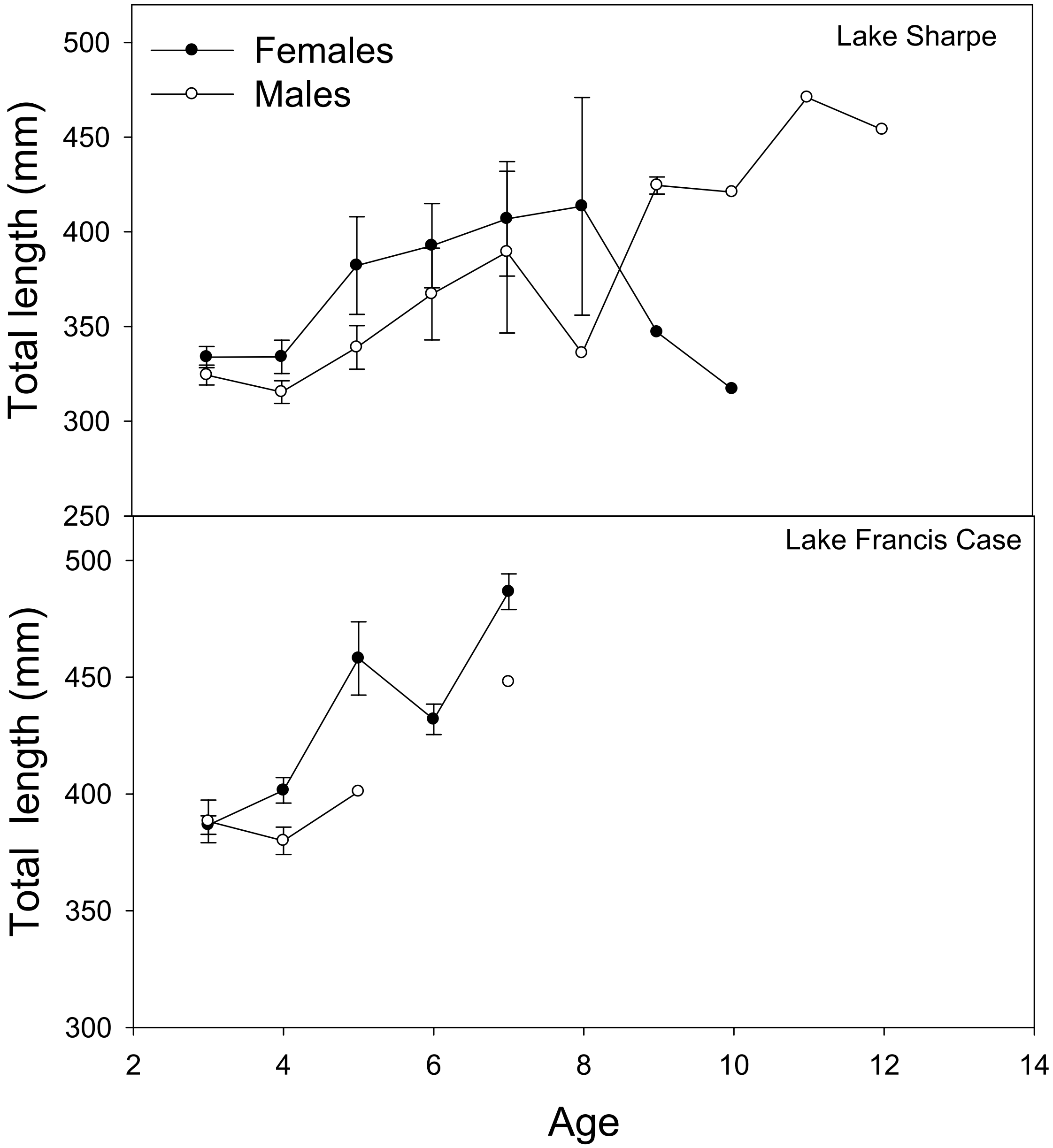

Figure 4-3. Mean length (±SE) at time of capture by age group for male and female gizzard shad collected from Lakes Sharpe and Francis Case during April and May 2004.

Chapter 5.

Summary and Research Needs

My research addressed several aspects of sauger population ecology that were needed to better understand sauger conservation. I determined that sauger naturally hybridize with walleye in Lakes Sharpe, Francis Case, and Lewis and Clark. Hybridization was relatively low in Lakes Sharpe and Francis Case (4%), whereas hybridization in Lewis and Clark Lake (21%) was quite high. Fortunately for sauger, the high hybridization rate in Lewis and Clark was skewed toward walleye, suggesting that reproductive barriers influencing hybridization are more resistant for sauger as compared to walleye. Recruitment of hybrids appeared to be affected by different environmental factors than recruitment of the parental species in Lewis and Clark Lake. Stronger than average hybrid year classes were predicted to occur during years with warmer than average temperature and reduced mainstem Missouri River discharge. In contrast, sauger and walleye recruitment was predicted to be higher than average during years when temperatures were warmer, and/or tributary inputs from the Niobrara River were decreased during the early life history of sauger. However, this relationship for parental recruitment was confounded by an interaction wherein warmer years would still allow higher recruitment, even if tributary inputs were moderate to high. Recruitment of sauger and walleye in Lake Sharpe appeared to be affected primarily by temperature, with warmer years resulting in above average recruitment. Overall, results from recruitment modeling suggested that manipulating water releases in reservoirs to facilitate warmer temperatures (e.g., by discharging warmer surface water through dams) during the early life history of sauger may enhance recruitment success of sauger. This measure could be implemented if sauger populations experience future declines.

Sauger spawned in much different locations in Lewis and Clark Lake than I predicted based on earlier studies. Previous studies indicated that sauger spawned near Fort Randall Dam in the Lewis and Clark system, where an abundance of suitable spawning habitat (i.e., gravel and cobble) remains. However, all transmittered sauger in my study spawned >40 km downstream from Fort Randall Dam, in the emerging delta habitat. This marked shift highlighted the potential importance of an emerging novel ecosystem of Missouri River reservoirs– deltas. This habitat maintains fluvial processes, including channel meandering, connectivity with the floodplain, and complex habitat, all of which have been identified as critical for restoring riverine function and creating habitat more suitable for sauger in riverine sections of the Missouri River basin. The Lewis and Clark delta has developed at a much faster pace than other reservoirs because of the relatively large size of the Niobrara River watershed (the primary source of sediments) in relation to the relatively small size of Lewis and Clark Lake, but the same process is occurring in Lakes Sharpe (Bad River delta) and Francis Case (White River delta), as well as all reservoirs ever constructed. Results from my study indicate that the emergence of these deltas may enhance sauger spawning habitat in other reservoir systems, contributing to continued population stability. Moreover, the larger implications of these results were that emerging deltas may provide habitat and function more similar to historic riverine conditions and should be further explored in riverine management and conservation.

Gizzard shad experienced remarkably consistent recruitment (no missing year classes) and very little annual variability in year-class strength (near constant annual mortality). As such, gizzard shad are no longer at risk for extirpation from low overwinter survival, as predicted by earlier studies conducted shortly after reservoir formation. In fact, the gizzard shad cohorts that I studied recruited consistently across a range of winters and reservoir conditions (i.e., normal flows, droughts, and floods), suggesting that reservoir conditions have changed as these systems aged, allowing age-0 gizzard shad to survive winters. Gizzard shad larvae (<20 mm) were consistently sampled throughout the upper two thirds of Lakes Francis Case and Sharpe from June through early August, indicating a wide hatching window and correspondingly wide availability (i.e., appropriately sized for gape-limited predators) as prey for predators such as sauger. Hipple Lake, a small backwater lake in the upper section of Lake Sharpe was identified as a potentially important source of larval gizzard shad in this system. Larval gizzard shad densities in this location were consistently high (often exceeding 1,000 individuals/m^3), as compared to generally low densities (<100 individuals/m^3) found elsewhere in Lake Sharpe and in Lake Francis Case. The wide availability of gizzard shad larvae combined with consistent recruitment of cohorts into the population indicate that gizzard shad are a favorable prey type for predators such as sauger in Missouri River reservoirs.

My study addressed many previously unknown and poorly understood aspects of sauger population ecology in Missouri River reservoirs, but many questions were also generated. Although this study identified several large-scale patterns (e.g., hybridization), specific mechanisms governing these patterns were not identified. Furthermore, some mechanisms identified in recruitment modeling (e.g., temperature during the early life history) are likely proximate mechanisms representing perhaps several ultimate factors influencing recruitment success of sauger. These trends point to a need to more fully understand the basic ecology of Missouri River reservoirs so as to better link to specific processes of interest to management and conservation. This study also highlighted the potential importance of emerging habitats on the conservation and management of Missouri River biota. These areas offer exciting areas of future research. Below I describe several specific research questions generated from my work.

Research needs

1) Natural hybridization between sauger and walleye was documented in Lakes Sharpe and Francis Case, and was particularly high in Lewis and Clark Lake. Understanding the basic reproductive ecology of these two species would greatly increase our understanding of both the extent of hybridization and the common directionality of this phenomenon (introgression was higher for walleyes than sauger). Research should focus on natural reproductive barriers and how they are breaking down between these two predators in these systems.

2) The low sample size of *Sander* cohorts (few individuals >age 4) that prevented recruitment modeling in Lake Francis Case highlights another potentially important factor influencing sauger populations in this system. The relatively young ages of adults suggests that exploitation may be truncating population age structure through increased fishing mortality. Studies quantifying natural and fishing mortality, combined with population modeling, would provide a better understanding of the potential role of exploitation in structuring sauger (and walleye) populations in Lake Francis Case.

3) Reservoir deltas such as the large and growing delta on Lewis and Clark Lake provided an interesting opportunity for future research. These areas are obviously important for sauger spawning, but because of their dynamic nature (i.e., riverine function more similar to the historic Missouri River), these locations may be important for conservation of other Missouri River biota. Because deltas are relatively novel features of reservoir landscapes, few studies have examined their potential role in riverine restoration, native fish conservation, etc. Thus, future research examining seasonal fish use (e.g., spawning habitat), biodiversity, and general function of these areas could have substantial implications for future management of the Missouri River.

4) The presence of isolated reservoir deltas highlights another future research need-connectivity of reservoirs. If deltas provide emerging habitats important for

native fish conservation, enabling fish to move between these patches within the reservoir landscape may be important. Currently, fish movement is limited to downstream directions, with upstream movement restricted by dams. Constructing fish passageways bypassing dams would connect these habitats and allow for the upstream movement of fish. I realize that a delicate balance is needed in connecting these systems as the furthest downstream dam (Gavins Point) currently restricts the upstream movement of nonindigenous Asian carps and other potential invasive species into upstream areas. One compromise might be to begin connecting upstream systems such as Lewis and Clark and Francis Case (via fish passage through Fort Randall Dam), but leave Gavins Point as is to function as a barrier.

5) The consistent recruitment of gizzard shad year classes examined in my study indicates that juvenile gizzard shad are now able to survive winters. However, the specific mechanism(s) influencing this survival is unknown. One potential factor allowing age-0 gizzard shad to survive their first winter may be the presence of artesian wells and the potential importance of thermal refuge. Identification of larger wells, and documentation of the use of these locations by overwintering gizzard shad would improve our understanding of how gizzard shad survive winters.

6) Adult gizzard shad population structure in Lewis and Clark Lake is still unknown. Future researchers should examine habitats not thoroughly covered during my study, such as deepwater areas within the reservoir and the Niobrara River as potential locations to adequately sample adult gizzard shad.

7) The very high densities of gizzard shad larvae in Hipple Lake as compared to the lower densities observed elsewhere suggest that this location may be an important source of gizzard shad for Lake Sharpe. Future research that can track the movement of larvae from Hipple Lake into Lake Sharpe, and perhaps even into Lake Francis Case, as well as quantify the contribution of larvae into the overall gizzard shad population would allow us to better understand the early life history of gizzard shad in this system.