Long-Term Data Suggest Potential Interactions of Introduced Walleye and Smallmouth Bass on Native Sauger in Four Missouri River Impoundments

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Abstract

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Keywords

Lake Francis Case, Lake Lewis and Clark, Lake Oahe, Lake Sharpe, long-term trend data, occupancy modeling

Disciplines

Aquaculture and Fisheries | Ecology and Evolutionary Biology | Natural Resources Management and Policy

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Surveys

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Keywords: Lake Francis Case; Lake Lewis and Clark; Lake Oahe; Lake Sharpe; long-term trend data; occupancy modeling

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Introduction

Sauger Sander canadensis is an important sport fish species throughout its native range. A top tier predator, the Sauger is closely associated with turbid lotic systems (Scott and Crossman 1973). As with many native species, alterations of habitat and biological communities through time may have had detrimental effects. The impoundment of reservoirs in Sauger native habitat and the transition from a lotic to lentic system, with attendant sport fish stockings, have the potential to negatively affect Sauger populations.

Sauger were once common throughout the Missouri River basin (Bailey and Allum 1962; Jones 1963; Cross 1967). Human alterations of the Missouri River, starting in the early 1900s and peaking with the construction of six major main-stem dams, were associated with declines in Sauger abundance and distribution. Proposed mechanisms driving declining trends include habitat alteration, competition and/or hybridization with Walleye Sander vitreus, angler harvest, and/or competition with Smallmouth Bass Micropterus dolomieu (Galat et al. 2005). Declining trends in Sauger abundance were readily apparent in free-flowing stretches of the Missouri River, as well as in main stem Missouri River reservoirs following impoundment (Nelson and Walburg 1977). However, little research has focused on the long-term population trends of Sauger after the initial studies, which finished soon after the closure of the Missouri River impoundments in the mid- to late 1900s.

In South Dakota, Sauger are readily harvested by anglers. When the Missouri River reservoirs were initially filled, Sauger were an important sport fish (Nelson and Walburg 1977). Below Oahe Dam from July 1959 to March 1960, >31,000 Sauger were harvested (Bailey and Allum 1962). Similarly, nearly 72,000 Sauger were harvested below Gavins Point Dam in 1958 (Orr 1962). These Sauger sport fisheries soon substantially declined; however, populations were thought to stabilize soon thereafter. Now, anecdotal evidence suggests that the Sauger sport fishery has continued to decline over the past 30 y. Generally, it was noted that fewer Sauger were being sampled or caught by anglers in fewer places. These anecdotes, along with the lack of recent study, motivated our examination of the long-term trends of Sauger in South Dakota’s main stem Missouri River reservoirs. Given the diversity of habitats between reservoirs, we were also concerned with both abundance and distribution trends.

To document changes of these important sport fisheries through time, we decided to use a multifaceted approach. Our objectives were to 1) determine whether Sauger abundance was declining using long-term standardized gillnet surveys; 2) determine whether Sauger occupancy was declining, as an indicator of possible within-reservoir range contraction, and 3) use long-term creel surveys to document potential concurrent changes in angler catch and harvest of Sauger. We replicated these analyses with Walleye and Smallmouth Bass. There is controversy as to the effects of Walleye and Smallmouth Bass on Sauger, so describing their population and occupancy trends may prove useful in explaining potential changes in Sauger population characteristics.

Study Site

The Missouri River is the longest river in North America, flowing 3,768 km and draining 1,371,017 km² through a network of 47 tributaries with drainage basins >1000 km² (Galat et al. 2005). The South Dakota portion of the Missouri River is impounded, forming Lakes Oahe, Sharpe, Francis Case, and Lewis and Clark in rural central South Dakota (upstream to downstream; Figure 1). All six of the major Missouri River impoundments can be classified as “large” compared with other North American reservoirs. Lake Oahe is the second largest of these six impoundments on the Missouri River and extends from Riverdale, North Dakota to Pierre, South Dakota. At normal pool, the South Dakota portion of Lake Oahe has a surface area of ~145,000 ha with a mean depth of ~19 m and a maximum depth of 67 m. Lake Sharpe is the second smallest Missouri River impoundment extending from Oahe Dam to Big Bend Dam. Lake Sharpe has a surface area of ~41,000 ha, with mean and maximum depths of ~15.2 and 42.6 m, respectively. Lake Lewis and Clark is the smallest and furthest downstream reservoir on the Missouri River and extends from Big Bend Dam to Fort Randall Dam. At normal pool, Lake Francis Case has a surface area of ~41,000 ha, with mean and maximum depths of 15.2 and 42.6 m, respectively. Lake Lewis and Clark is the smallest and furthest downstream reservoir on the Missouri River. Lewis and Clark Lake extends from Fort Randall Dam to Gavins’ Point Dam. At normal pool, Lewis and Clark Lake has a surface area of 10,500 ha, and is considerably shallower than the other three study reservoirs with mean and maximum depths of 5.0 and 16.7 m, respectively.

Each of the reservoirs follow the typical productivity pattern for reservoirs (Fincel 2011). The upper reaches are considered cold, oligotrophic riverine conditions largely dictated by the cold-water releases of upper reservoirs. As you move downstream in the reservoirs, transition zones appear and local inputs serve to increase nutrient inputs and algal and zooplankton...
production increases. In some cases, productivity can approach mesotrophic or borderline eutrophic states in these transition zones (Fincel 2011). Then by the lower end of the reservoirs, nutrients are largely used up and algal and zooplankton density declines appreciably. Lake Oahe experiences a strong thermocline in all years and Lake Francis Case experiences a thermocline in most years. However, Lake Sharpe and Lewis and Clark rarely see the development of a thermocline (Fincel 2011).

All the reservoirs have similar species assemblages with Walleye, Smallmouth Bass, and Sauger as primary predator species. All reservoirs also contain low abundances of Northern Pike Esox lucius, Crappy spp. Pomoxis, and White Bass Morone chrysops. All the reservoirs have also been stocked with Rainbow Trout Oncorhynchus mykiss and/or Brown Trout Salmo trutta in the cold water tailraces in various years. Lake Oahe is unique in that Chinook Salmon O. tshawytscha have been stocked annually since the late 1980s. Common prey fish species include Gizzard Shad Dorosoma cepedianum, Yellow Perch Perca flavescens, Spottail Shiner Notropis hudsonius, Emerald Shiner N. atherinoides, and various age-0 sport fish (Fincel 2011; Fincel et al. 2014).

Figure 1. Current depiction of the Missouri River impoundments in central South Dakota, USA. Black rectangles represent locations of dam structures.

Methods

Population surveys

The South Dakota Department of Game, Fish, and Parks (SDGF&P) conducted standard coolwater-fish population surveys from 1984 through 2016 on Lakes Francis Case and Lewis and Clark (n = 32 y), 1985 through 2016 on Lake Oahe (n = 31 y), and 1986 through 2016 on Lake Sharpe (n = 30 y). The department conducted surveys in August (Lakes Oahe and Sharpe) and September (Lakes Francis Case and Lewis and Clark) at standard sites (Lake Oahe, n = 9; Lake Sharpe, n = 6; Lake Francis Case, n = 9, Lake Lewis and Clark, n = 4). At each site, surveyors deployed three gillnets in a straight line from anchor to anchor, pulled nets taught, and set them overnight (~20 h) and on the bottom within depth zones of 0–10 m and 10–20 m for 3–6 nets/site. Surveyors randomly set nets parallel and transverse to bottom contour lines. If part or all of the gillnet was unfishable due to wind or wave action, surveyors disregarded the partial catch in that net as not influencing estimates of catch rates, and they reset the gillnet as soon as possible. Gillnets were constructed of multifilament nylon and were 91 m × 2 m, had a 0.5
hanging ratio, with 15-m panels with sequentially increasing bar mesh sizes: 13, 19, 25, 32, 38, and 51 mm. Surveyors kept effort constant within each reservoir for the study period. Surveyors identified captured fish to species using common phenotypic characteristics; and measured, weighed, and removed otoliths from a subset of individuals for age and growth analysis. We omitted any potential Sander phenotypic hybrids from this study.

We assumed that standardized use of gillnetting throughout the study period would represent temporal variation of each species’ underlying abundance, and that species-specific differences in catchability did not change through time (Fincel et al. 2015). We analyzed within-reservoir abundance trends with linear regressions, and examined correlations between annual abundance. Smallmouth Bass were not caught in standard surveys until 2011 in Lake Lewis and Clark and infrequently after that. Thus, we did not analyze trend data for Smallmouth Bass in this reservoir. Nonetheless, anecdotal evidence suggests an increasing population since the 1980s when Smallmouth Bass were stocked but the magnitude is not currently discernible.

Variability in species abundance is common in these types of long-term studies. Thus, reviewing the general trends is important because variability around the mean is generally high as strong or weak year-classes emerge. Moreover, yearly sampling conditions such as high winds or inclement weather can greatly influence abundance estimates further increasing yearly variability. Thus, caution must be taken when interpreting year-to-year variability in long-term gillnet data.

**Occupancy modeling**

Occupancy modeling has been used to assess habitat use by various species (Moore et al. 2017), estimate species co-occurrence (Richmond et al. 2010; Peoples and Frimpong 2015), or evaluate detection probabilities between various sampling gears (Moore et al. 2017). Occupancy analyses assume 1) closure of the sample population, 2) no false detections at a sampling location, and 3) detection of a species is independent between sampling locations. Moreover, yearly sampling conditions such as high winds or inclement weather can greatly influence abundance estimates further increasing yearly variability. Thus, caution must be taken when interpreting year-to-year variability in long-term gillnet data.

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We transformed our gillnet abundance data to presence–absence data. Consequently, a site that was sampled with 6 gillnets and caught the desired fish on the first, third, and fourth net would result in a detection history (\( h_i \)) of 101100. A single individual captured in any of the nets would result in an occupied site. Detection and occupancy probabilities are formulated simultaneously; hence, the \( h_i = 101100 \) would report the site as occupied but the species was not detected by the second, fifth, or sixth net. Thus, the probability of occupancy for that site would be 1 and the detection probability calculated therein:

\[
\Psi_i = P_1 \times (1-P_2) \times P_3 \times P_4 \times (1-P_5) \times (1-P_6)
\]

where \( \Psi \) is the site-specific occupancy probability, \( P_j \) is the probability of detecting the species in the \( j \)th survey given it is present. Sites where no fish were caught still have a probability of occupancy despite no individuals being caught. For this analysis, we combined several years of standardized surveys in a robust design similar to that of Pollock’s robust design for mark–recapture studies (Pollock 1982), where each year represents a primary sampling period and each sampling site represents secondary periods (MacKenzie et al. 2003). Thus, 3 y of survey data for a single site could yield a detection history of

\[
h_i = ‘101100 000000 100100’
\]

where a space was inserted between yearly sampling events. From this, we know that the species was present in the first and third year but either not detected or absent during the second year. We can then use our parameters of detection–nondetection data through probability statements to assign a probability of 1) occupied but not detected, or 2) not occupied during the second year of sampling. Detection probabilities are unlikely to remain constant between primary sampling periods (MacKenzie et al. 2003); therefore, we used year-specific detection probabilities in our occupancy model. We also assumed colonization and extinction probabilities to be time-dependent, so we did not bind these parameters. Our specific question is to identify trends in occupancy of these three sport fish, so we modeled and/or compared no covariate or co-occurrence trends. Here we assume sampling locations encompass the various habitats available within the reservoirs and present the results as lake-wide occupancy estimates (percent of the lake occupied by a particular species) through time.

**Creel surveys**

The SDGF&P conducted standardized creel surveys yearly from 1991 through 2016 for Lakes Oahe, Sharpe, and Francis Case \( n = 25 \) y. The SDGF&P reported catch rate and harvest for all years, but reported total catch only in Lake Sharpe starting in 1992. The SDGF&P conducted creel surveys on Lake Lewis and Clark in 1994,

The SDGF&P patterned angler use and sport-fish harvest surveys conducted on Lake Oahe and Lake Sharpe prior to 2003 after a study designed by Schmidt (1975). Sampling included aerial boat and shore angler counts along with angler interviews at lake access sites. The SDGF&P conducted ∼12 flights monthly for the open-water angling season (May–October), 6 weekday, and 6 weekend or holiday flights. The SDGF&P selected interview dates using a stratified random design based on the assumption of differential levels of fishing pressure for weekdays, weekend days, and holidays with approximately half of the creel shifts occurring on weekends or holidays. Additionally, the SDGF&P separated lakes into three (Lake Oahe) or two (Lake Sharpe) approximately equal-sized zones with equal interview effort captured within each zone. Creel clerks spent between 12 and 18 d creeling within each zone each month, routinely capturing between 400 and 600 interviews lake-wide per month. The SDGF&P assigned specific lake-access areas selected for angler interviews using a stratified random design whereby creelers were given a starting location and roved to adjacent access points in an attempt to gather as many interviews as possible. The SDGF&P included incomplete trips in this analysis and applied zone and monthly estimates of trip length, catch, and harvest estimates to zone and monthly estimates of pressure counts to determine lakewide estimates using Creel Application Software. For a more detailed description of aerial count, angler interview, and data expansion techniques, see Stone et al. (1994) and Fincel et al. (2012a).

Beginning in 2003, a bus-route survey design (Jones and Robson 1991) replaced aerial counts on Lake Sharpe to increase the statistical reliability of the pressure estimates similar to that used for Lake Francis Case (Soupir et al. 2006; Sorenson and Knecht 2010). For Lake Francis Case and Lake Sharpe (2003 through 2016), the SDGF&P used a bus route design (count interval method) to estimate angler catch, harvest, and pressure. Here, the creel clerk waits for a specified period of time proportional to the expected pressure at the site, and then travels to the next location. Upon arrival to an access location, creel clerks would record the initial number of shore anglers and boat trailers present and departure times of anglers. The creel clerk would also interview anglers as they left the access site to document catch, harvest, and time spent fishing. Lakes were divided into three (Lake Sharpe) or five (Lake Francis Case) logical zones with starting routes, travel direction, and creel shift beginning and ending times randomized for each creel shift. The SDGF&P included incomplete trips in this analysis. The SDGF&P calculated pressure estimates based on day type, access site, route probability, work shift probability, wait time at the access site, total route length, and user ratio using the Robson and Jones method (Robson and Jones 1989). The SDGF&P applied estimated angling pressure for each zone and month to the angler interviewed-derived catch and harvest estimates to determine lakewide estimates using Creel Application Software.

On Lake Lewis and Clark, creel surveys were infrequent and conducted by South Dakota Game, Fish, and Parks as well as the Nebraska Game and Parks Commission. They used a random stratified roving creel survey design to gather catch data from anglers described for Lake Oahe (Malvetuto 1996). They collected instantaneous pressure counts at both access sites (methods described for Lake Francis Case) and using a plane (methods described for Lake Oahe). Similar to other reservoirs, they applied zone-specific monthly data collected from angler interviews to pressure counts to determine lake wide estimates using Creel Application Software. For a more detailed description of Lake Lewis and Clark creel surveys, see Bouska and Longhenry (2010).

Obviously, there is an inherent bias associated with creel surveys (Pollock et al. 1994; McCormick et al. 2013). In particular, when comparing species-specific harvest results, care must be taken. For instance, Sullivan (2003) found anglers exaggerated Walleye catches as a function of catch rates. Additionally, inherent bias in the angler preference for harvest is apparent on the Missouri River reservoirs, with most anglers frequently harvesting Walleye, fewer anglers preferring to harvest Sauger, and even fewer harvesting Smallmouth Bass (Fincel et al. 2012a, 2012b). Additionally, angler attitudes regarding Smallmouth Bass must be taken into account. In the mid-2000s, a protected slot limit was enacted on Smallmouth Bass but this regulation was generally unaccepted by anglers and the regulation was eventually removed in 2012 (Fincel et al. 2015). Thus, care must be taken when interpreting estimates of catch and harvest of Smallmouth Bass in our long-term creel surveys.

Results

Population surveys

In general, Sauger abundance is declining (negative slope) on Lakes Oahe, Sharpe, and Lewis and Clark but increasing on Lake Francis Case (positive slope; Table 1, Figure 2; Table S1, Supplemental Material). Interestingly, Walleye abundance is also declining on Lakes Oahe, Sharpe, and Francis Case (Figure 3). Smallmouth Bass abundance is increasing in Lakes Oahe, Sharpe, and Francis Case (Figure 4). Sauger and Walleye correlation coefficients were negative in Lakes Oahe and Francis Case (Table 2) as a result of inverse population trends (Figures 2 and 3), whereas positive coefficients in Lakes Sharpe and Lewis and Clark reflected the concurrent decline. Sauger and Smallmouth Bass correlation coefficients were all negative (Table 4). This is likely due to the declines in Sauger abundance (Figure 2) and concurrent increases in Smallmouth Bass (Figure 4).
Table 1. Linear regression coefficients for mean catch per unit effort (CPUE; #/net) and occupancy (ˆψ) of Sauger, Walleye, and Smallmouth Bass for four Missouri River reservoirs (Lakes Oahe [1985–2016], Sharpe [1986–2016], Francis Case [1984–2016], and Lewis and Clark [1984–2016]) in South Dakota, USA. Bold text represents significant model fit (α ≤ 0.2).

<table>
<thead>
<tr>
<th></th>
<th>Sauger</th>
<th></th>
<th>Walleye</th>
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</tr>
<tr>
<td>Lake Lewis and Clark</td>
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<td>0.05</td>
<td>238.8</td>
<td>−0.12</td>
<td>0.08</td>
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<tr>
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<td>&lt;0.01</td>
<td>−312.3</td>
<td>0.16</td>
<td>0.30</td>
</tr>
<tr>
<td>Lake Sharpe</td>
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<td>80.5</td>
<td>−0.04</td>
<td>0.22</td>
</tr>
<tr>
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<td>10.9</td>
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<td>0.01</td>
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<tr>
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<tr>
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<td>12.4</td>
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<td>0.12</td>
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<td>15.4</td>
<td>−0.01</td>
<td>—</td>
</tr>
</tbody>
</table>

Occupancy modeling

Trends in occupancy suggest a long-term decrease in site occupancy within all four reservoirs for Sauger (Table 1; Table S2, Supplemental Material). However, Lake Francis Case exhibited the slightest Sauger decline of all reservoirs. In general, Walleye site occupancy is decreasing on Lakes Sharpe and Francis Case but increasing on Lake Lewis and Clark. Walleye occupied 100% of the sites throughout the duration of the analysis on Lake Oahe; hence, we performed no trend analysis. Lakes Oahe, Sharpe, and Francis Case exhibited increasing trends in site occupancy for Smallmouth Bass.

Creel surveys

Sauger exhibited a decreasing trend in angler harvest (#), catch (#), and catch rate (#/angler-h) on Lakes Oahe and Sharpe and a decreasing trend in harvest (#) and harvest rate (#/angler-h) on Lake Lewis and Clark (Table S3, Supplemental Material). Contrary, Lake Francis Case documented an increase in Sauger harvest, catch, and catch rate (Table 3, Figure 5). Both Walleye and Smallmouth Bass exhibited increasing trends in harvest, catch, and catch rate in Lakes Oahe, Sharpe, and Francis Case (Figure 6 and 7), and an increasing trend in harvest and harvest rate on Lake Lewis and Clark (Figure 8). Regression coefficients are presented in Table 3 for Lakes Francis Case, Sharpe, and Oahe; whereas, Lewis and Clark coefficients are in Table 4 to account for different temporal range.

Discussion

It appears Sauger are declining in three of the four South Dakota Missouri River impoundments over the past 30 y. Both site occupancy rates and overall abundance indicate the population is declining and spatial distribution contracting. The only exception to these observations was in Francis Case where probability of occupancy declined despite increases in Sauger abundance. Angler information mirrors that from standard surveys, with catch and harvest of Sauger decreasing through time on Lakes Oahe, Sharpe, and Lewis and Clark. Also, like the standard surveys, Sauger show an increasing trend in catch and harvest on Lake Francis Case. Both fish population and angler accounts are therefore providing complimentary information.

Lake Francis Case exhibited the only positive abundance trends for Sauger in South Dakota Missouri River reservoirs. Looking more finely into the Francis Case data set, we found that a single site was showing marked increases in Sauger catches. That site was in close proximity to the White River, a large, turbid tributary. Although Sauger are becoming rarer throughout the lake, it appears this area has been promoting the increased abundance of Sauger in Lake Francis Case. This is unsurprising because Sauger are spatially associated with the turbid, flowing tributaries that approximate their original riverine habitat. The White River flows year round but can have seasonal floods that pour fine sediments into the lake. This unique feature could likely aid in the persistence of Sauger in Lake Francis Case. This tributary’s turbid water could be used as a spawning and foraging location. For instance, the majority of Sauger spawning was thought to take place below the Powder River tributary of the Yellowstone River, which is a major source of fine sediments (Rehwinkel et al. 1978). The largest spawning aggregation of Sauger in the Little Wind River system occurred just downstream of Beaver Creek, a large source of warm turbid water (Kuhn et al. 2008). The turbid waters entering Lake Francis Case could also be facilitating increased foraging efficiency for Sauger whose eyes are adapted to highly turbid, low-light situations (Ali and Anctil 1977). Moreover, growth of Sauger in the Missouri River varies among latitudes and subsequent degree growing days, suggesting improved growth in warmer waters (Braaten and Guy 2002). The warm water discharge could be providing a thermal refuge unique to Lake Francis Case.

The overarching concern regarding Sauger declines in the Missouri River basin has been habitat alteration. Sauger populations in the Montana portion of the basin have shown a similar decline to South Dakota populations over a similar time scale (McMahon and Gardner 2001). Sauger are native to large rivers and the anthropogenic changes found throughout the Missouri...
River are extensive. Large dams, changes in hydrological regimes, decreased sediment loads and turbidity, changes to water temperature patterns, etc., all pose concerns to native Sauger. The highly migratory nature of the Sauger is thought to be severely affected by barriers. In the unimpounded Yellowstone River, Sauger migrations between spawning and home areas were the longest documented (Jaeger et al. 2005), with downstream migrations common. These behaviors, especially upstream migrations, are largely limited when systems are impounded like the Missouri River reservoirs.

Sauger hybridization with Walleye may also be contributing to the declining trends. In Lake Lewis and Clark, hybridization rates rose from 10% to 21% of Sander spp. between 1995 and 2002 (Van Zee et al. 1996; Graeb et al. 2010). If hybridization is increasing between the two similar species, it is likely cumulative hybridization effects may be limiting Sauger populations. For instance,
Arnold and Hodges (1995) and Utter (2003), both suggest reduced fitness of introgressed populations. Other *Sander* populations within the Missouri River basin have shown high hybridization rates, including 22% in the Missouri River below Ft. Peck reservoir, 20% in Lake Sakakawea in North Dakota, and 20% in the upper reach of the Missouri River in Montana (Billington et al. 2006); however, a more recent study showed 1.9% hybridization in Montana reaches, demonstrating that hybridization varies spatially and temporally across the Missouri River (Bingham et al. 2012). South Dakota rates were all documented >15 y ago, so hybridization between the two species may have changed since that time. Reviewing current trends in hybridization between Sauger and Walleye may prove beneficial in explaining current Sauger declines.

We documented mixed Walleye abundance trends in the Missouri River reservoirs. Lakewide occupancy has

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**Figure 3.** Estimated abundance (catch per unit effort; filled circles) and lake occupancy (open circles) of Walleye collected from standard gillnet surveys in four South Dakota Missouri River impoundments from 1984 to 2016. Long dashes and short dashes represent trend lines for Sauger *Sander canadensis* abundance and lake occupancy, respectively.
remained high in all reservoirs, with Walleye present in nearly 100% of the sites annually. This may be a function of intermittent yet adequate recruitment as originally noted by Nelson and Walburg (1977), who described the establishment of the Walleye fishery in the years following reservoir closures. The overall trend is similar to Ivan et al. (2011), who attributed the long term increase in Lake Huron Walleye abundance during 1980–2008 to stockings and then successful natural reproduction.

Walleye have readily been blamed for widespread declines of Sauger throughout its range. Although animosity exists, little direct evidence has been published solidifying this mechanism. Diet overlap has been shown in some sympatric populations but can differ depending on prey composition and availability. In the middle Missouri River, diet overlap between Walleye and Sauger was high in spring and summer, but declined in autumn when benthic fish were more abundant in

Figure 4. Estimated abundance (catch per unit effort; filled circles) and lake occupancy (open circles) of Smallmouth Bass Micropterus dolomieu collected from standard gillnet surveys in four South Dakota Missouri River impoundments from 1984 to 2016. Long dashes and short dashes represent trend lines for Sauger Sander canadensis abundance and lake occupancy, respectively.
Smallmouth Bass. In lakes and reservoirs, diet similarity between Walleye and Sauger appears to be more variable. Lake Erie Sauger consumed primarily Freshwater Drum Aplodinotus grunniens and other demersal prey fishes with macroinvertebrates composing <1% of the diet by weight (Rawson and Scholl 1978). In contrast, diets of similar-sized Walleye contained approximately 30% macroinvertebrates (Rawson and Scholl 1978). A comparative study of Walleye and Sauger diets in Lake of the Woods, Minnesota, showed that Sauger consumed more demersal fish such as trout–perch Percopsis omiscomaycus and fewer invertebrates than Walleye (Swenson and Smith 1976). In contrast, Walleye consumed more pelagic prey that included Yellow Perch, Cisco Coregonus artedi, and Rainbow Smelt Osmerus mordax (Swenson and Smith 1976; Swenson 1977). In three of the South Dakota Missouri River impoundments, diet breadth and variability varied for Walleye and Sauger, with potential overlap in Lake Lewis and Clark but less so in Lake Francis Case or Lake Oahe (Fincel et al. 2016). However, in most studies, diet items of Walleye and Sauger were not limiting and, thus, direct competition is rarely confirmed. Moreover, Haxton (2015) documented separation of Sauger and Walleye by depth strata while foraging. This may be due to eye morphology differences (Ali and Anctil 1977), and subsequent habitat partitioning based on ambient light levels from either depth or water clarity (Ali and Anctil 1968). Ickes et al. (1999) documented strong habitat partitioning both by depth but also spatially between the two species. This habitat partitioning between the two species could explain the apparent diet overlap but lack of direct competition.

Smallmouth Bass were stocked throughout the Missouri River reservoirs in the 1980s. These populations appear to be increasing, and may be influencing Sauger abundance and distribution. In the three reservoirs experiencing Sauger declines, Smallmouth Bass are becoming more abundant and more widespread. Moreover, a weak negative correlation exists between the species in all three reservoirs examined. Although research focusing on direct competition between the two species is lacking, there is some evidence that Smallmouth Bass competition may be negatively influencing Sauger populations (Galat et al. 2005). To our knowledge, no study has directly measured diet or resource overlap of the two species. In lieu of Sauger–Smallmouth Bass diet comparisons, Walleye and Smallmouth Bass diet studies suggest Smallmouth Bass diets tend to include more benthic invertebrates from wider taxa compared with Walleye. In Spirit Lake, Iowa, Liao et al. (2002) found Yellow Perch were consistently the dominant component of Walleye diets, whereas Smallmouth Bass diets included substantial percentages of littoral invertebrates, mainly crayfish (Cambarus spp). It appears Smallmouth Bass exhibit a more littoral–benthic diet compared with Walleye, and this littoral–benthic diet is more similar to the Sauger diets discussed previously. Thus, it is plausible that Sauger and Smallmouth Bass may show more diet overlap than either species does with Walleye. Although this is not direct evidence of diet overlap, it at least gives us a reason to question the extent of diet overlap of Sauger and Smallmouth Bass. Additionally, direct consumption of Sander spp. by Smallmouth Bass has been documented in many studies. Johnson and Hale (1977), Bacula (2009), and Welhner et

### Table 2. Linear regression coefficients of species-specific harvest, catch, and catch rates for Lakes Francis Case, Sharpe, and Oahe in South Dakota, USA, during 1991–2016. Bold text represents significant model fit ($\alpha \leq 0.2$).

<table>
<thead>
<tr>
<th>Species</th>
<th>Intercept</th>
<th>Slope</th>
<th>R²</th>
<th>P</th>
<th>Harvest (#/angler/h)</th>
<th>Catch (#/angler/h)</th>
<th>Catch rate (#/angler/h)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sauger Sander canadensis</td>
<td>0.00</td>
<td>0.90</td>
<td>0.00</td>
<td>0.00</td>
<td>0.50</td>
<td>0.16</td>
<td>0.00</td>
</tr>
<tr>
<td>Walleye Sander vitreus</td>
<td>0.04</td>
<td>0.60</td>
<td>0.04</td>
<td>0.20</td>
<td>0.06</td>
<td>0.22</td>
<td>0.17</td>
</tr>
<tr>
<td>Smallmouth Bass Micropterus dolomieu</td>
<td>0.00</td>
<td>0.90</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>

### Table 3. Linear regression coefficients of species-specific harvest, catch, and catch rates for Lake Lewis and Clark, South Dakota, USA, from years 1994, 1995, 2000, 2001, 2005, 2006, 2009 and 2010. Bold text represents significant model fit ($\alpha \leq 0.2$).

<table>
<thead>
<tr>
<th>Species</th>
<th>Intercept</th>
<th>Slope</th>
<th>R²</th>
<th>P</th>
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Table 4. Correlation matrices of Sauger Sander canadensis (SAR), Walleye Sander vitreus (WAE), and Smallmouth Bass Micropterus dolomieu (SMB) gillnet abundance (catch per unit effort) for four Missouri River reservoirs (Lakes Oahe [1985–2016], Sharpe [1986–2016], Francis Case [1984–2016], and Lewis and Clark [1984–2016]) in South Dakota, USA. Values represent correlation coefficients (r).

<table>
<thead>
<tr>
<th>Lake Oahe</th>
<th>Lake Sharpe</th>
<th>Lake Francis Case</th>
<th>Lake Lewis and Clark</th>
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<tbody>
<tr>
<td>SMB</td>
<td>WAE</td>
<td>SAR</td>
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<tr>
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<td>SAR</td>
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<td>1.000</td>
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</table>

Figure 5. Harvest (#), catch (#), and catch rate (#/angler/h) of Sauger Sander canadensis by anglers in Lakes Oahe, Sharpe, and Francis Case, South Dakota, from 1991 through 2016.
al. (2010), all found low levels of predation on Sander spp. by Smallmouth Bass. In Spirit Lake Iowa though, young Walleye comprised 24% of Smallmouth Bass diets (Liao et al. 2004). However, in most cases it was assumed that the low abundance of Smallmouth Bass at the time meant that population-level effects would be minimal. Nonetheless, with Smallmouth Bass populations increasing in three of the four reservoirs, potential interactions between Smallmouth Bass and Sauger should be further studied.

In conclusion, it appears that Sauger are continuing to decline in the Missouri River impoundments; however, small areas are continuing to produce numerous individuals. The exact mechanism for Sauger decline is unknown but many questions arise as to the effects of further habitat degradation and interactions with other sport fish in these systems. Currently, no protective regulations have been placed on Sauger in South Dakota water bodies.

Supplemental Material

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Figure 6. Harvest (#), catch (#), and catch rate (#/angler/h) of Walleye Sander vitreus by anglers in Lakes Oahe, Sharpe, and Francis Case, South Dakota, from 1991 through 2016.
supplemental material. Queries should be directed to the corresponding author for the article.


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Found at DOI: https://doi.org/10.3996/122018-JFWM-115.S3 (17 KB DOCX).

Figure 7. Harvest (#), catch (#), and catch rate (#/angler/h) Smallmouth Bass *Micropterus dolomieu* by anglers in Lakes Oahe, Sharpe, and Francis Case, South Dakota, from 1991 through 2016.

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