

Competition Potential between Saugers and Walleyes in Nonnative Sympatry

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Abstract.—Sauger *Sander canadensis* populations throughout North America have exhibited declines over the past few decades. Various factors may contribute to the reduced population abundance of saugers in the middle Missouri River of Montana, including interspecific competition with walleyes *Sander vitreus*. We compared the seasonal migrations, habitat use, and diets of both species in the middle Missouri River to assess competition potential. Before the presumed spawning period, 96% of saugers and 57% of walleyes migrated as far as 264 kilometers downstream. After spawning, both species returned to previously occupied river reaches and demonstrated site fidelity during the nonmigratory season. Habitat use by saugers and walleyes was similar at three hierarchical spatial scales. Diet overlap was high during the spring and summer and moderate during autumn. Resource overlap of saugers and walleyes in the middle Missouri River of Montana suggests that the competition potential between these species is high, which may preclude the recovery of native sauger populations where resources are limiting.

Saugers *Sander canadensis* are native top-level predators in large, turbid rivers of the central United States and Canada (Scott and Crossman 1973) and have undergone declines in abundance and distribution throughout their range (Nelson and Walburg 1977; Hesse 1994; Pegg et al. 1997; McMahon and Gardner 2001). Saugers have declined in Montana in the Yellowstone River and in the section of the middle Missouri River between Great Falls and Fort Peck Reservoir (McMahon and Gardner 2001); the species is currently listed as a Montana Species of Special Concern (MNHP 2004). The decline of saugers in both rivers was originally attributed to a drought in the mid-1980s (McMahon and Gardner 2001). Increased flows in the 1990s corresponded to a rebound of the lower Yellowstone River population (Jaeger 2005); however, the abundance of the middle Missouri River population has remained low (Gardner 2005). The difference in recovery of the two systems suggests that

another mechanism may have confounded the effects of drought on saugers and is continuing their suppression in the Missouri River. Anecdotal evidence from biologists suggests that walleyes *S. vitreus*, which are nonnative to the middle Missouri River, are competing with saugers for resources. Thus, we investigated competition potential between saugers and walleyes to conserve native saugers in the middle Missouri River of Montana.

Saugers and walleyes were both present in the middle Missouri River before the drought of the mid-1980s, but walleyes comprised less than 0.01% of the combined sauger and walleye catch (Berg 1981). Walleyes comprised 30.8% of the combined sauger and walleye catch in 2003 (Gardner 2005). Although walleyes are not believed to be the direct cause of the decline in sauger abundance after the drought (McMahon and Gardner 2001), drought conditions may have caused changes in river habitat that allowed the expansion of the walleye population.

Dams on the middle Missouri River may contribute to the current abundance of both species and may affect resource overlap and competition potential between them. Saugers and walleyes are spatially segregated in nonaltered systems or where both species are native (Swenson 1977; Rawson and Scholl 1978; Schlick 1978; Billington et al. 1997), whereas both species

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exhibit habitat overlap in altered systems (Rawson and Scholl 1978; Gangl et al. 2000). Consequently, the current altered condition of the middle Missouri River may increase habitat overlap between saugers and walleyes and increase interspecific competition potential.

Three conditions must be met for significant interspecific competition to occur: (1) two species must use a common resource, (2) the resource must be limiting, and (3) there must be negative effects (e.g., decreased growth rates, population abundance, or another metric correlated with fitness; Crowder 1990). Ideally, competition is assessed using field or laboratory experiments that demonstrate repeatable changes in the growth or abundance of species when resources or competitors are manipulated (Crowder 1990). However, experimental manipulation of highly migratory species (e.g., saugers and walleyes) in a large system such as the Missouri River is not logistically feasible. Laboratory experiments may also be unrealistic because they do not incorporate environmental variability and other biological interactions. Thus, information on resource overlap between saugers and walleyes would be a useful first step towards understanding competition potential between these species. For our study, we defined competition potential as high overlap of food and habitat resources. These resources are most commonly partitioned by fish species to minimize competition (Ross 1986), and thus high overlap of food and habitat resources would indicate competition potential.

The purpose of this study was to assess the competition potential between saugers and walleyes and understand how competition affects sauger recovery in the middle Missouri River, Montana. The specific objectives were to (1) compare the movements of saugers and walleyes during the migratory and nonmigratory seasons, (2) assess habitat overlap between the species at several spatial scales, and (3) calculate the overlap of sauger and walleye diets by season. Based on the hypothesis that closely related species in a nonnative assemblage are more likely to compete because they have not had sufficient time to coevolve and partition resources, we predicted that saugers and walleyes would exhibit high resource overlap in the middle Missouri River, Montana.

Study Area

The study was conducted in north-central Montana and included the middle Missouri River and its tributaries between Morony Dam (river kilometer [rkm] 3,388, measuring from the mouth of the Missouri River) and the headwaters of Fort Peck Reservoir (about rkm 3,000; Figure 1). The majority of the work

was conducted on the section from Fort Benton (rkm 3,337) to Coal Banks Recreation Area (rkm 3,267) because saugers declined markedly in this area and walleyes are relatively abundant.

Eight upstream hydroelectric dams affect the in-stream habitat of the middle Missouri River. The 50 km of river downstream of Morony Dam is probably clearer and colder than under historical conditions because of hypolimnetic water release from Morony Dam. Additionally, the upstream dams moderate the peaks and troughs of the historical hydrograph, although the timing of the discharges is similar to that in the past. Average peak discharge (741 m³/s) has decreased by 29% and average base flow (114 m³/s) has increased by 42% since construction of the most recent upstream dam in 1958 (USGS 2006). Morony and Fort Peck dams are also barriers that inhibit migratory species. Substrate is primarily gravel, cobble, and boulder in the upper reaches and transitions to primarily sand downstream of Fred Robinson Bridge.

Methods

Seasonal migrations.—We captured 31 adult saugers (350–1,600 g) and 29 adult walleyes (600–1,750 g) via electrofishing and implanted each with a radio transmitter in the autumn of 2003 and 2004 and recorded their seasonal migrations in 2004 and 2005. Transmitters weighed 10.7 g and were programmed to transmit daily from 0800 hours to 2000 hours in 2003. In 2004, transmitters were on 24 h/d so that nocturnal movements could be recorded. The start times of transmitters were delayed until mid-February to preserve battery life and enable fish to be tracked through the subsequent summer. Saugers and walleyes were tagged in three river reaches—(1) Coal Banks (rkm 3,268–3,284), Loma (rkm 3,284–3,320), and Fort Benton (rkm 3,320–3,347)—which represented the area where sauger abundance markedly decreased. Anesthetic and surgical techniques generally followed those by Hart and Summerfelt (1975) and Summerfelt and Smith (1990). Saugers and walleyes were monitored at least 30 min following surgery before being released.

Radio-tagged saugers and walleyes were located from February through October in 2004 and February through mid-November in 2005. An airplane was used to locate fish during the winter and early spring when saugers and walleyes were dispersed over a large area (about 300 rkm) and because the river was frozen. Boat tracking began after fish returned from the spawning migration and were aggregated within a shorter river reach (about 90 rkm). Saugers and walleyes were located monthly by plane during February and March

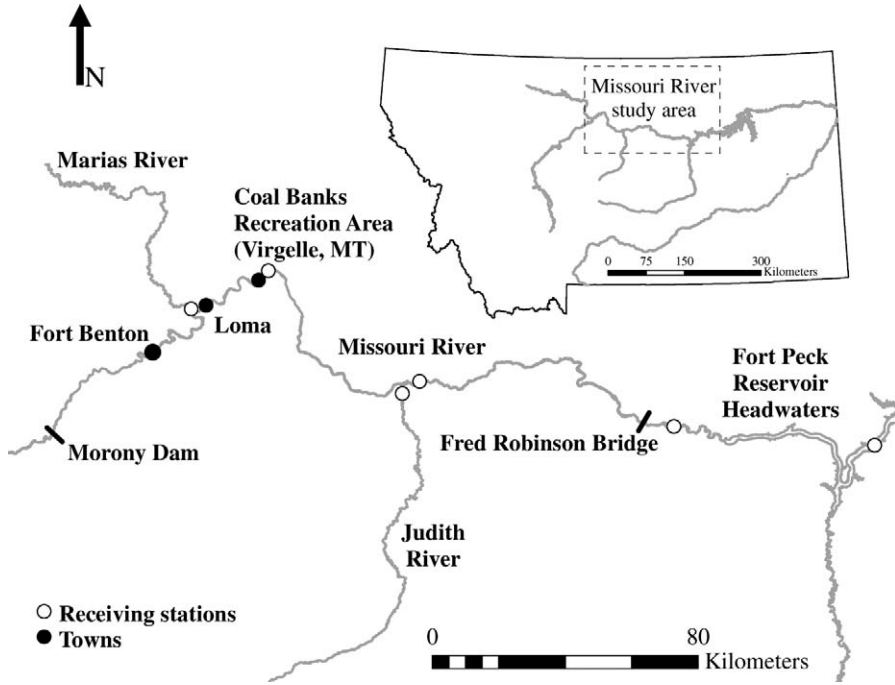


FIGURE 1.—Map of the middle Missouri River study area.

and at least biweekly by plane or boat from May through mid-August in 2004 and May through July in 2005. Boat tracking accuracy, estimated by locating a hidden transmitter, was 2–5 m. Autonomous receiving stations were installed at strategic locations to supplement mobile tracking (Figure 1). Radio-tagged fish caught and reported by anglers also contributed to location data. About 56% of locations were determined by boat, 26% by plane, and 18% were recorded by autonomous receiving stations.

Migration data were grouped into migratory and nonmigratory seasons for analysis, based on sauger and walleye life history information (Scott and Crossman 1973). The migratory season (November through May) included the movements to overwinter areas, migration to spawning grounds, spawning, and postspawning migration. The nonmigratory season included the remainder of the year. As the migration times of individual fish differed, each fish was categorized into the appropriate season based on its movement. We used the return proximity of a fish after the migration season to the reach where it was tagged (i.e., Fort Benton, Loma, or Coal Banks) to determine site fidelity. The length of river used by saugers and walleyes during the nonmigratory season was compared using a Wilcoxon two-sample test because data were nonnormally distributed. Mean daily discharge

data were collected from the U.S. Geological Survey (USGS) monitoring station at Virgelle, Montana, and temperature data were obtained from the USGS station near Fred Robinson Bridge (Figure 1).

Habitat use in nonmigratory season.—Habitat use was classified and compared between saugers and walleyes at three hierarchical spatial scales: channel unit, channel unit quadrant, and specific fish location. These scales were chosen to represent an array of habitat resolutions available to saugers and walleyes. Habitat use was only evaluated during the nonmigratory season. The nonmigratory season used for habitat analyses was defined similarly to that for movements.

Channel units were classified into seven categories (bluff pool, terrace pool, riprap pool, scour pool, channel crossover, perennial secondary channel, and seasonal secondary channel) based on differences in flow, depth, and substrate type. This enabled us to compare our results with those from previous sauger research on the Yellowstone River (Jaeger et al. 2005). Bluff pools were located at the valley margin and were formed by deflection of the river against exposed bedrock (Rabeni and Jacobson 1993). Terrace pools were created by scour from glacially deposited alluvium and colluvium (Jaeger et al. 2005). Riprap pools were primarily located at the valley margin and were formed by scour against anthropogenic materials

(i.e., riprap and bridge abutments). Scour pools were created from scour through river-deposited alluvium (Rabeni and Jacobson 1993). Channel crossovers included run and riffle habitats and were located where the thalweg crossed from one side of the river to the other. Perennial secondary channels contained water throughout the year. Seasonal secondary channels were disconnected from the main channel at either the inlet or outlet at some point during the year. Channel units were determined using geologic maps, aerial photos, and habitat notes taken in the field; these units were delineated using ArcGIS 9.0 Geographic Information System (GIS) software (ESRI 2004). Availability was quantified as the number of river kilometers of each channel unit between rkm 3,242 and 3,357, which was the river section used by fish during the nonmigratory season. Because many of the channel units in this study were relatively large (e.g., up to 5 km in length and up to 300 m wide) and because saugers and walleyes could be segregated within a channel unit yet have a high overlap value, we divided channel unit types that were used most frequently by both species into four equal-sized quadrants and calculated overlap at the channel unit quadrant scale to examine habitat overlap more precisely. For both channel units and channel unit quadrants, one-way chi-square log-likelihood tests and Manly selection ratios (Manly et al. 2002) with 95% simultaneous Bonferroni confidence intervals were calculated for saugers and walleyes via FishTel 1.4 software (Rogers and White 2007). Although some expected values used for chi-square analyses were less than the common recommendation of 5, chi-square tests are robust to smaller expected values (Roscoe and Byars 1971; Lawal and Upton 1984).

Point estimates of habitat were measured at sauger and walleye locations determined by boat tracking. Water clarity was quantified at each location using a Secchi disk mounted to a meter-long dowel. Two transects (one perpendicular and one parallel to river flow) were established to quantify the depth of the fish location in relation to the surrounding depths (i.e., relative depth). Five substrate measurements were taken at each fish location: at the fish location, 5 m upstream, 5 m downstream, 5 m left, and 5 m right. Substrate was classified as fines (0–0.6 mm), gravel and cobble (0.6–254 mm), or boulder (>254 mm) by feeling the substrate with a probe constructed of 1.3-cm electrical conduit. Secchi depth data were compared between species using a Wilcoxon two-sample test because data were nonnormally distributed. A repeated-measures (with individual fish as the repeated variable) analysis of variance (ANOVA) was used to compare relative depth for saugers versus walleyes, where individual fish

were the experimental units. Differences in substrate use were assessed with a chi-square test.

Diet sampling.—We used electrofishing to sample 278 saugers and 131 walleyes with respect to diet during the nonmigratory season in the middle Missouri River between Fort Benton and Coal Banks Recreation Area. The nonmigratory season was subdivided into spring (May and June), summer (July and August), and autumn (September to November) periods for diet analysis. Diets were collected throughout this reach to correspond with the group of fish used for movement and habitat analyses. Stomach contents were removed using a gastric lavage, fixed in 15% formalin, and transferred to 70% ethanol for long-term preservation. Identifiable fish were categorized to species and macroinvertebrates were identified to order. Prey fish unidentifiable to species were placed in an “unidentifiable fish” category. Empty stomachs and those containing only detritus, sediment, or vegetation were considered empty. Prey fish length (mm) and wet weight (g) were recorded; macroinvertebrates were counted and wet-weighted by order.

Diet overlap was quantified using prey weight and Pianka's niche overlap measure (Pianka 1973), which varies from 0 (no overlap) to 1.0 (complete overlap). Overlap indices were estimated using bootstrapping methods (Ricklefs and Lau 1980; Smith 1985). One sauger and one walleye diet were randomly chosen from the respective sample populations, an overlap value was calculated 5,000 separate times, and these estimates were averaged to obtain the overlap index. The larger sample size allowed a measure of variability to be estimated and reduced the effect of outliers on the overlap value (Ricklefs and Lau 1980; Smith 1985). We checked the assumptions of all statistical tests before running analyses and set significance at $\alpha = 0.05$. We report the Satterthwaite approximation for degrees of freedom for all tests that did not meet the assumption of equal variances (Satterthwaite 1946).

Results

Seasonal Migrations

We relocated 26 saugers 275 times and relocated 24 walleyes 187 times. The difference in the number of fish with relocation data versus the number of fish originally tagged was due to 7 missing fish and 12 mortalities. Three additional saugers and six walleyes were radio-tagged during the summers of 2004 and 2005 to increase sample size. We relocated 23 saugers and 18 walleyes during the migratory season. Relocations per fish during the migratory season averaged 7 (SE = 0.7) for saugers and 5 (SE = 0.7) for walleyes. We used 21 saugers and 14 walleyes for analyses during the nonmigratory season; all had 3 or more

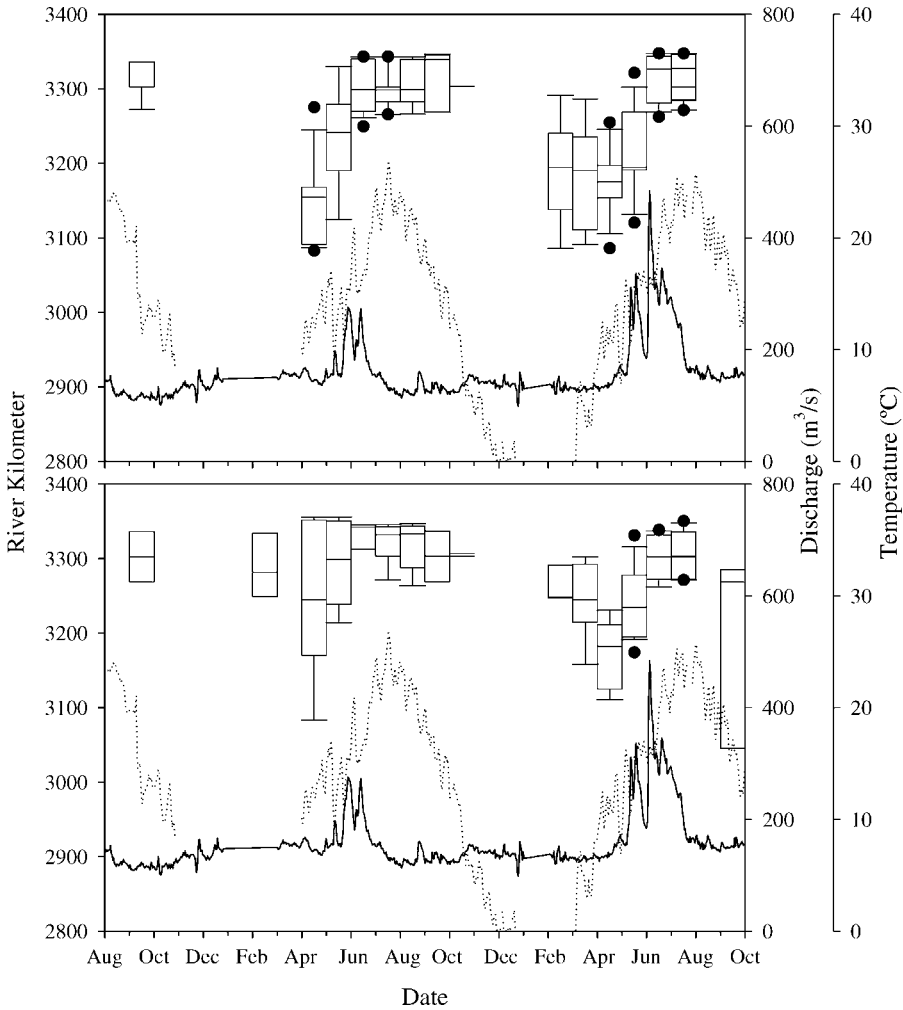


FIGURE 2.—Sauger (top panel) and walleye (bottom panel) movements in relation to discharge (solid lines) and water temperature (dotted lines) in the middle Missouri River, Montana, from August 2003 to October 2005. Radio tag location data are grouped by month. The solid lines within the boxes represent the medians, the boundaries of the boxes the 25th and 75th percentiles, the whiskers the 10th and 90th percentiles, and the circles the 5th and 95th percentiles. All box plots represent at least three locations.

locations during the nonmigratory season. Relocations per fish during the nonmigratory season averaged 5 (SE = 0.2) for saugers and 5 (SE = 0.5) for walleyes.

The movements of saugers and walleyes were generally similar during the migratory season and corresponded to changes in water temperature and river discharge (Figure 2). The majority of saugers ($N = 22$) and walleyes (14) moved extensive distances downstream as water temperatures cooled and discharge diminished between autumn and mid-May. Downstream sauger migrations varied from 34 to 254 km (mean = 170 km, SE = 10.7), and walleye migrations varied from 14 to 264 km (mean = 130 km, SE = 22.1).

Both species were located downstream during the presumed spawning period in April and early May and began returning upstream from late April through May as water temperature and discharge increased (Figure 2).

Saugers and walleyes exhibited site fidelity after the migratory season and both species occupied relatively small areas during the nonmigratory season. All saugers ($N = 23$) and 44% of the walleyes ($N = 8$) returned after the migratory season to the river reach (i.e., Fort Benton, Loma, or Coal Banks) where they were caught and tagged the previous year. The amount of river used during the nonmigratory season did not

TABLE 1.—Mean percent use (SEs in parentheses) of channel unit types by saugers and walleyes in the middle Missouri River, Montana, and channel unit availability during the nonmigratory season, 2004 and 2005.

Channel unit type	Availability	Use	
		Sauger	Walleye
Bluff pool	13	45 (0.10)	45 (0.11)
Terrace pool	13	3 (0.02)	8 (0.06)
Riprap pool	3	18 (0.08)	15 (0.08)
Scour pool	16	14 (0.06)	4 (0.03)
Channel crossover	23	10 (0.05)	15 (0.06)
Perennial secondary channel	18	8 (0.05)	3 (0.02)
Seasonal secondary channel	14	2 (0.02)	10 (0.06)

differ significantly between saugers (mean = 2.15 km, SE = 1.20) and walleyes (mean = 1.05 km, SE = 0.24; Wilcoxon two-sample test; $P = 0.92$). The variability of the sauger mean was highly influenced by a single fish that used 24 km of river during the nonmigratory season.

Nonmigratory Season Habitat Use

Channel crossovers were the most available channel unit habitat and riprap pools were the least available (Table 1). Bluff pools and riprap pools were the most frequently used channel unit types by both species. Saugers and walleyes did not select channel unit types in proportion to their availability ($\chi^2 = 405.89$, $df = 126$, $P < 0.0001$ for saugers; $\chi^2 = 298$, $df = 84$, $P < 0.0001$ for walleyes), and both species selected similar channel units (Figure 3). Downstream, outside bend quadrants of bluff pool channel units were used most frequently by saugers (46%) and walleyes (67%). Saugers and walleyes did not select bluff pool quadrants in proportion to their availability ($\chi^2 = 86.53$, $df = 33$, $P < 0.0001$ for saugers; $\chi^2 = 61.14$, $df = 24$, $P < 0.0001$ for walleyes) and positively selected similar quadrants (Figure 4). Downstream, outside bend quadrants of riprap pool channel units were also primarily used by saugers (60%) and walleyes (75%). Saugers and walleyes did not select riprap pool quadrants in proportion to availability ($\chi^2 = 27.76$, $df = 12$, $P = 0.006$ for saugers; $\chi^2 = 28.41$, $df = 9$, $P = 0.0008$ for walleyes) and positively selected similar quadrants (Figure 4).

Point estimates of habitat at sauger and walleye locations were similar. Mean relative depth of locations did not differ significantly between species within channel unit types ($F_{1, 65.4} = 3.35$, $P = 0.07$); however, relative depth differed between channel unit types ($F_{6, 119} = 5.82$, $P < 0.0001$; Table 2). Substrate use was not significantly different between species ($\chi^2 = 0.1068$, $df = 2$, $P = 0.95$). Gravel and cobble

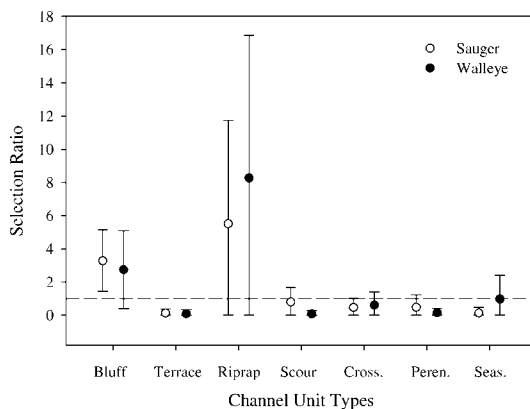


FIGURE 3.—Selection ratios and 95% simultaneous Bonferroni confidence intervals of channel unit types during the nonmigratory season for saugers and walleyes in the middle Missouri River, Montana, 2004 and 2005. The channel units are bluff, terrace, riprap, and scour pools, channel crossovers (cross.), perennial secondary channels (peren.), and seasonal secondary channels (seas.). Values greater than 1 (dashed line) indicate positive selection, values less than 1 negative selection, and values of 1 selection in proportion to availability.

substrates were used most frequently (saugers: mean = 76%, SE = 4.3; walleyes: mean = 71%, SE = 5.9), whereas fine substrates (saugers: mean = 16%, SE = 3.9; walleyes: mean = 23%, SE = 5.6) and boulder substrates (saugers: mean = 8%, SE = 3.2; walleyes: mean = 6%, SE = 2.0) were used less frequently. Mean Secchi depth at fish locations did not differ between saugers (mean = 0.46 m, SE = 0.02) and walleyes (mean = 0.49, SE = 0.03; Wilcoxon two-sample test, $P = 0.76$).

Diets

Diet items of saugers and walleyes were similar; overlap varied by season and was lowest in autumn (Table 3). Unidentified fish were common in diets of both species during all seasons (Table 3). Stomachs were empty in 28% of the saugers and 33% of the walleyes sampled during spring. Spring diet overlap was high (mean Pianka overlap value = 0.72, SE = 0.003) between saugers and walleyes and they similarly consumed emerald shiners and stonecats. Diet items during spring in the "other" category were brook sticklebacks *Culaea inconstans* and crayfish (family Astacidae) for walleyes and longnose suckers *Catostomus catostomus* and flathead chub *Platygobio gracilis* for saugers. Stomachs were empty in 25% of saugers and 23% of walleyes during summer. Diet overlap was high during the summer (mean Pianka overlap value = 0.71, SE = 0.003); however, one large

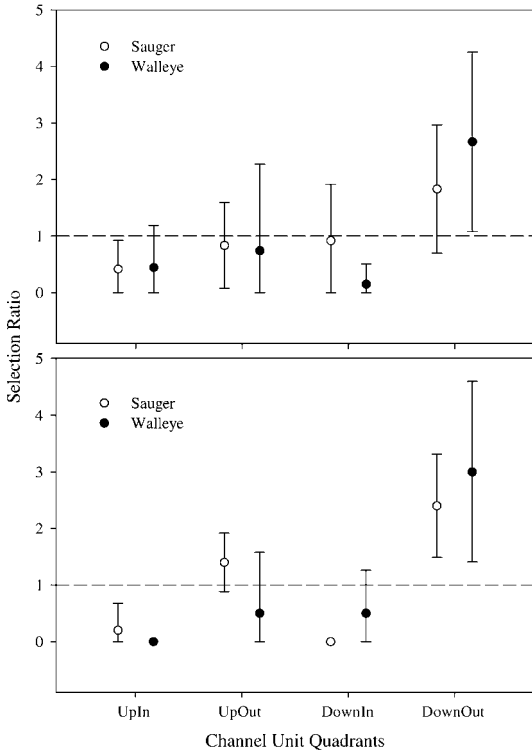


FIGURE 4.—Selection ratios and 95% simultaneous Bonferroni confidence intervals of bluff pool quadrants (top panel) and riprap pool quadrants (bottom panel) during the nonmigratory season for saugers and walleyes in the middle Missouri River, Montana, 2004 and 2005. The quadrants are upstream inside bend (UpIn), upstream outside bend (UpOut), downstream inside bend (DownIn), and downstream outside bend (DownOut). Values greater than 1 indicate positive selection, values less than 1 negative selection, and values of 1 selection in proportion to availability.

smallmouth bass *Micropterus dolomieu* (total length = 166 mm, weight = 83 g) consumed by a walleye highly influenced the overlap value. The mean Pianka overlap value was 0.95 (SE = 0.0008) when the smallmouth bass was excluded. Saugers and walleyes primarily

consumed stonecats during the summer and less frequently consumed emerald shiners, macroinvertebrates, and mottled sculpin. The “other” category during summer included longnose suckers for saugers compared with smallmouth bass, crayfish, and rainbow trout for walleyes. In autumn, 37% of sauger and 19% of walleye stomachs were empty, and diet overlap was moderate (mean Pianka overlap value = 0.49, SE = 0.003). Saugers primarily consumed stonecats in autumn; walleyes also consumed stonecats, but emerald shiners and western silvery minnow were the primary diet items. Diet items in the “other” category during autumn were smallmouth bass for saugers and longnose suckers for walleyes.

Discussion

The seasonal migrations of saugers in the middle Missouri River were similar in length and direction (up to 254 km downstream) to those of saugers in the Yellowstone River (<300 km downstream; Jaeger et al. 2005) but differed from those in other systems where saugers migrated upstream (Nelson 1968; Pitlo 1989; Pegg et al. 1997; Gangl et al. 2000) or migrated short distances downstream (Siegwarth 1993). Interestingly, saugers in both the middle Missouri and Yellowstone rivers also migrated to river reaches with similar geologic features during the presumed spawning period. In the middle Missouri River, saugers used a section of river in the Judith River Geologic Formation, which is associated with rocky ledges that are resistant to erosion (MBMG 2002). Similarly, saugers in the Yellowstone River selected the Tullock and Lebo Members of the Fort Union Formation, which form bedrock outcrops (Jaeger et al. 2005). Saugers are known to use rocky substrates and bedrock reefs during the spawning season throughout their range (Nelson 1968; St. John 1990; Hesse 1994; Jeffrey and Edds 1999). Saugers in the middle Missouri and Yellowstone rivers also exhibited site fidelity after spawning by returning upstream to areas occupied the previous year (Jaeger et al. 2005). The similarity of

TABLE 2.—Percent relative depth of sauger and walleye radio tag locations by channel unit type during the nonmigratory season in the middle Missouri River, Montana, 2004 and 2005.

Channel unit type	Saugers		Walleyes		P
	Mean (SE)	Range	Mean (SE)	Range	
Bluff pool	49 (3.9)	24–63	50 (4.1)	29–74	0.84
Terrace pool	80 (2.7)	65–95	73 (3.4)	69–76	0.67
Riprap pool	54 (3.5)	48–66	63 (7.3)	52–77	0.27
Scour pool	70 (8.5)	39–100	55 (2.6)	53–58	0.39
Channel crossover	70 (8.7)	43–94	55 (8.7)	25–87	0.25
Perennial secondary channel	61 (1.6)	58–64	55 (9.0)	46–64	0.43
Seasonal secondary channel	100 (0)	100–100	70 (5.8)	59–78	

TABLE 3.—Diet percent by weight of saugers and walleyes during the spring, summer, and autumn periods in the middle Missouri River, Montana. The number of stomachs sampled of each species by season is denoted by *N*.

Diet item or <i>N</i>	Spring		Summer		Autumn	
	Saugers	Walleyes	Saugers	Walleyes	Saugers	Walleyes
Emerald shiner <i>Notropis atherinoides</i>	8.7	11.7	7.0	6.5	9.8	22.1
Macroinvertebrates	0.0	0.1	0.0	0.3	0.0	0.0
Mottled sculpin <i>Cottus bairdii</i>	6.4	0.0	10.4	4.3	0.0	0.0
Stonecat <i>Noturus flavus</i>	36.1	48.0	58.9	33.4	31.8	5.3
Western silvery minnow <i>Hybognathus argyritis</i>	19.2	0.0	9.2	1.3	13.9	29.4
Other species	7.1	4.1	0.2	31.8	10.2	7.2
Unidentified fish species	22.4	36.1	14.2	22.3	34.2	36.0
<i>N</i>	92	39	135	71	51	21

sauger movements in these two rivers suggests that anthropogenic moderation of middle Missouri River discharge has not greatly affected sauger migratory behavior; however, historical migratory patterns of middle Missouri River saugers are not completely known.

Although the movements of walleyes in the middle Missouri River differed from those of walleyes in other systems, they had the same temporal and spatial scales as those of saugers in the middle Missouri River. The extensive downstream migration of walleyes (>200 km) before the spawning season and the return migration upstream are not known to occur in any other system. However, upstream migrations of walleyes from lakes into rivers and wholly within rivers have been documented (Paragamian 1989; Pitlo 1989; DiStefano and Hiebert 2000), with some migrations exceeding 150 km (Priegel 1967). Short downstream migrations (5–10 km) by walleyes to spawning sites have also been reported (Siegwarth 1993) but are much less extensive than the distances recorded in this study. The overlap of walleye and sauger seasonal migrations in the middle Missouri River indicates that both species occupy the same river reaches at the same time of the year.

Walleyes selected bluff pools in proportion to availability, and both saugers and walleyes selected riprap pools in proportion to availability; however, the high use and relatively low availability of these channel unit types suggests that positive selection may have been detected if a larger sample size had been taken. Selection in proportion to availability was due to large confidence intervals, which are often a product of low expected values in chi-square tests and are most likely conservative (Roscoe and Byars 1971). Thus, a higher number of locations per fish (i.e., increased expected values) would probably result in smaller confidence intervals and may indicate positive selection of bluff and riprap pools by saugers and walleyes.

The use and positive selection of certain quadrants

within bluff and riprap pools by saugers and walleyes may be related to the microhabitat characteristics of those quadrants. Bluff pools are formed by impingement of the channel against resistant bedrock material, which scours and deepens the channel on the outside of the bend (Rabeni and Jacobson 1993). This scouring also erodes rocky substrates (primarily boulders) into the channel, particularly on the outside bend where the bank scour is occurring. Riprap pools are essentially man-made bluff pools, and they scour similarly by deepening the channel on the outside bend and recruiting rocky substrates to the river channel. The reason saugers and walleyes selected the downstream half of the outside bend may be flow. Secondary currents and bed shear stress are lowest near the downstream ends of river bend pools (Bridge and Jarvis 1982) so these areas may serve as a velocity refuge for saugers and walleyes. Spiral currents adjacent to the outside bank are also present at the downstream end of pools as the thalweg crosses over (Bridge and Jarvis 1982) creating additional velocity refuge. The lower velocities of downstream, outside bends combined with deep water and large, rocky substrates may contribute to the similar use and selection of these areas by saugers and walleyes.

Similar use and selection of channel units and channel unit quadrants suggests that saugers and walleyes overlap spatially in the middle Missouri River and have the potential to compete; however, habitat use was only assessed during the nonmigratory season. Understanding the seasonal variability of habitat use between species would yield a more complete picture of competition potential. Nevertheless, competition potential is probably high during the nonmigratory season and may influence the interactions between saugers and walleyes more strongly than during other seasons. Low discharge during the nonmigratory season directly affects the available habitat by limiting the amount of water. Thus, the potential for competition may increase as water levels drop and confine

saugers and walleyes to a smaller area. Increased water temperature during the nonmigratory season may also contribute to competition potential. Higher water temperatures increase the metabolic rate of walleyes (Cai and Summerfelt 1992) and may exacerbate competition between the species, assuming that saugers respond similarly to higher water temperatures. Higher metabolic rates increase the demand for food, which combined with the density increase of saugers and walleyes at low discharge during the nonmigratory season, may create higher competition potential during the nonmigratory season than in any other period of the year.

Diet overlap was high during the spring and summer, indicating competition potential for food resources. Diets of saugers and walleyes were also similar in other systems where they are sympatric (Priegel 1963; Swenson and Smith 1976; Fitz and Holbrook 1978; Mero 1992), although diet differences have also been observed (Rawson and Scholl 1978). Saugers and walleyes were assumed to be competing for food resources during June and July in Lake of the Woods, Minnesota, based on resource overlap and low prey availability (Swenson and Smith 1976). Competition decreased in August and September as prey abundance increased and saugers and walleyes were spatially separated (Swenson and Smith 1976). Diet overlap was high in our study during the spring (May and June) and summer (July and August) and habitats were similarly used by saugers and walleyes, which indicates high competition potential. Diet overlap during the autumn (September and October) was moderate, indicating decreased competition potential for food. Diet overlap results were temporally similar to those found in Lake of the Woods; however, information on prey availability by season in the middle Missouri River is needed to more thoroughly assess competition.

Habitat and food resources similarly used by saugers and walleyes undoubtedly fluctuate temporally and spatially in the middle Missouri River. The amount of available habitat fluctuates in response to changing discharge. Fish populations are also known to fluctuate both within and among years in response to varying discharge (Welcomme and Hagborg 1977). High-discharge events within years correspond to a greater density and biomass of fish, whereas low-discharge periods regulate the amount of fish surviving to the following year (Welcomme and Hagborg 1977). Thus, intensity of spring flooding in the middle Missouri River and the amount of flow during the base flow period may be related to prey fish population abundance and biomass. Discharge variability would directly affect the amount of prey available to saugers

and walleyes within and among years and may limit prey abundance, particularly during drought years.

Ecologically similar species will be influenced by the same resource limitations, and one species may be phenotypically favored (Wiens 1977). Walleyes grow to larger average sizes than saugers (Scott and Crossman 1973) and subsequently, have a larger average gape size. Thus, walleyes have the ability to consume larger prey items than saugers during periods of low prey-fish recruitment. Walleyes are also efficient predators that have drastically depleted prey fish populations in systems where they were introduced, leading to shifts in fish assemblage composition and competition for food resources with other piscivores (McMahon and Bennett 1996). The similarity in the diets of saugers and walleyes in the middle Missouri River suggests that both species consume similar prey, which may lead to food supply depletion and competition, especially during years of low prey abundance. Anthropogenic alterations to the middle Missouri River (i.e., dams) have affected the river by increasing water clarity in the tailrace and moderating the peaks and troughs in the hydrograph. Walleyes are better adapted and can feed more effectively than saugers at higher light conditions caused by increased water clarity (Ali and Ancil 1968). Additionally, walleyes are primarily adapted to lentic habitats (Scott and Crossman 1973) and may gain a competitive edge over saugers in rivers with anthropogenically moderated flow regimes. Saugers, which are primarily adapted to large rivers (Scott and Crossman 1973) with variable flow regimes, often decline numerically following the creation of reservoirs on such rivers (Nelson and Walburg 1977; St. John 1990; Hesse 1994).

Overall, the use of habitat and food resources was similar between saugers and walleyes in the middle Missouri River, indicating a potential for competition. However, understanding resource availability is a crucial component to actually deducing competition. Although not quantified in this study, resource availability fluctuates in aquatic systems (Wiens 1977) and may be especially pronounced in lotic systems where abiotic factors are an influential determinant of community structure (Townsend 1989). Accordingly, competition for resources among ecologically similar, sympatric species also fluctuates (Wiens 1977). Species with similar resource use are not likely to compete when resources are abundant, whereas competition will occur when resources are scarce (Wiens 1977). Resource availability is also related to the population abundance of the competing species. Population abundances lower than the amount required to fully utilize a scarce resource will not result

in competition. Nevertheless, fluctuations in the availability of similarly used habitat and food resources may result in periods where resources are limiting and competition is likely to occur between saugers and walleyes.

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