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Seasonal Movements, Habitat Use, Aggregation, Exploitation, and Entrainment of Saugers in the Lower Yellowstone River: An Empirical Assessment of Factors Affecting Population Recovery

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Abstract.—Migratory barriers, habitat loss, entrainment in irrigation canals, and overexploitation, especially at times of aggregation, have been suggested to explain the failure of Yellowstone River saugers *Sander canadensis* to return to historical abundances after a late-1980s decline that was attributed to drought. These factors are thought to affect saugers throughout their range and migratory large-river fishes in general. We characterized the seasonal movement patterns, habitat use, and aggregation of saugers and estimated movement, exploitation, and irrigation canal entrainment rates to test these hypotheses. Saugers aggregated near spawning areas in spring and subsequently dispersed 5–350 km to upstream home locations, where they remained for the rest of the year. Upstream movement was not overtly restricted by low-head diversion dams. During the spawning period, terrace and bluff pools, which are unique geomorphic units associated with bedrock and boulder substrate, were positively selected, while all other habitat types were avoided. Tributary spawning was rare. After moving to home locations, saugers used most habitat types in proportion to their availability but selected reaches in specific geologic types that allowed formation of deep, long pools. Exploitation occurred primarily in early spring and late autumn, was low annually (18.6%), and was not related to aggregation. Annual survival was high (70.4%). Entrainment in one irrigation diversion accounted for more than half of all nonfishing mortality. Therefore, habitat loss and overexploitation probably did not prevent sauger recovery, as the absence of migratory barriers allowed adult saugers unrestricted access to widely separated and diverse habitats and did not induce artificial aggregation. In other systems, population declines attributed to overexploitation during periods of aggregation may therefore have been caused fundamentally by migration barriers that created artificial aggregations.

Saugers *Sander canadensis* are among the most widely distributed of North American fishes; however, declines in distribution and abundance have resulted from rangewide habitat fragmentation and degradation (Rawson and Scholl 1978; Hesse 1994; Pegg et al. 1997; McMahon and Gardner 2001). Impoundment and subsequent flow management isolate saugers from important spawning and rearing habitats, reduce turbidity and temperature, and alter the timing and magnitude of the hydrograph from the natural regime in which saugers evolved (Hesse 1994; McMahon and Gardner 2001). Channelization reduces off-channel rearing habitats (Gardner and Berg 1980; Hesse 1994). Unrestricted access to widely separated and diverse habitat types throughout the year is critical to riverine fishes in general (Schlosser 1991; Fausch et al. 2002). The sauger's highly migratory nature (Collette et al. 1977; Penkal 1992; Pegg et al. 1997), propensity to spawn in only a few areas (St. John 1990; Penkal 1992), and reliance on a wide variety of habitats with natural temperatures and turbidities throughout their life history (Penkal 1992; Hesse 1994; Amadio et al. 2005) combine

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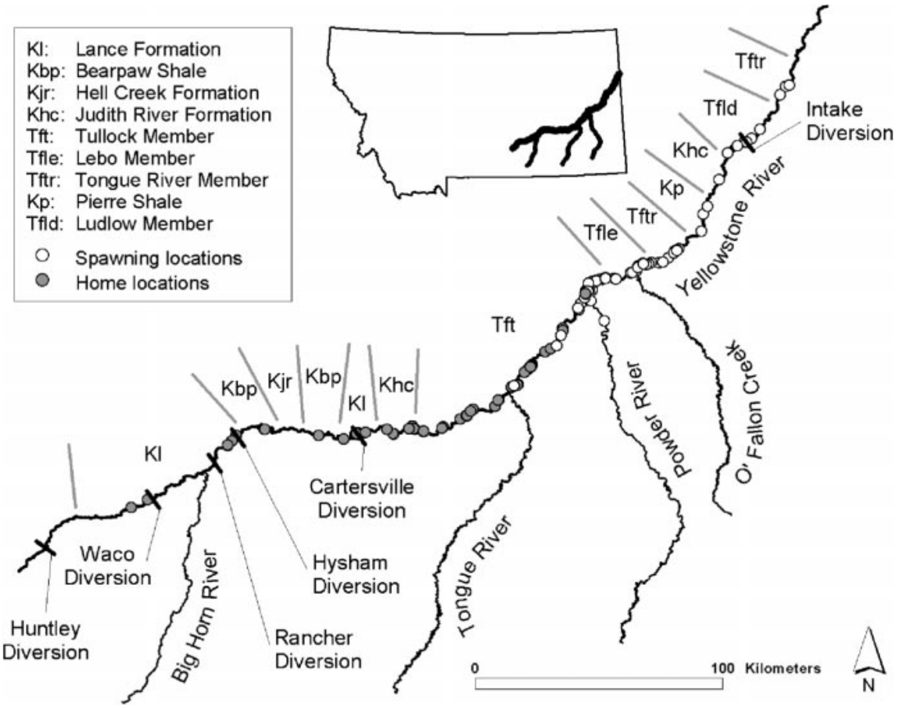

FIGURE 1.—Map of the lower Yellowstone River and major tributaries, diversion dams, and underlying geologic types showing the spawning and home locations of telemetered saugers during 2001–2003. Where overlap of location points occurs, outlying spawning and home locations are displayed to allow full representation of each distribution.

to make this percid species one of the most sensitive to habitat fragmentation and alteration (McMahon 1999). Rangewide declines in sauger abundances have also been attributed to overexploitation of aggregations (Nelson 1969; Hesse 1994; Pegg et al. 1996); however, most previous studies have implied that the apparent propensity of saugers to aggregate makes them susceptible to overexploitation. Effective management and mitigation of anthropogenic influences requires an understanding of the ecology of a species under natural conditions. However, almost all major river systems where saugers occur are altered to such an extent that research directed at achieving such an understanding is no longer possible.

The Yellowstone River retains a near-natural hydrograph and relatively pristine main-stem habitats (White and Bramblett 1993), making it the most suitable large river in which to examine the movements, habitat use, and other factors affecting sauger population abundance under natural conditions. Sauger abundance in the Yellowstone River declined to historical lows after a regionwide drought during 1987–1990 (McMahon and Gardner 2001). However, the failure of the sauger population to recover after five out of the seven subsequent years (1991–1997) displayed above-average spring–summer discharge suggested that factors in addition to discharge affected abundances (McMahon and Gardner 2001). Many of the same factors believed to affect saugers throughout their range (i.e., migratory barriers, habitat loss, and overexploitation during times of aggregation) were suggested to explain the failure of Yellowstone River saugers to return to historical abundances (McMahon and Gardner 2001). Entrainment in irrigation canals was also thought to affect recovery; over 67,000 saugers are entrained each year in the Intake Diversion Canal (Figure 1; Hiebert et al. 2000), the largest of six major diversions on the Yellowstone River. However, a lack of information regarding sauger exploitation and entrainment rates, specifically as they related to equally unknown seasonal movement and aggregation patterns and habitat use, made it difficult to assess the validity of these hypotheses and to effectively manage saugers in the Yellowstone

River (McMahon and Gardner 2001) and elsewhere.

Our objectives were to characterize seasonal movement patterns, habitat use, and aggregation and to estimate the movement, exploitation, and irrigation canal entrainment rates of the Yellowstone River adult sauger population. Objectives were directed at determining which factors (habitat fragmentation, loss of spawning habitat, overexploitation, or entrainment) prevented recovery of the Yellowstone River sauger fishery. Assessment of movement patterns, movement rates, and habitat use, which allowed characterization of seasonally important habitat types, provided an understanding of the extent to which diversion dams restricted sauger movement and fragmented seasonally important habitat types. Investigation of habitat use also allowed assessment of whether spawning habitat was limited. Description of seasonal aggregation patterns provided an understanding of the times and locations at which saugers were most susceptible to overexploitation; estimation of exploitation rates incorporating tag loss and angler nonreporting allowed accurate assessment of angler harvest. Estimation of entrainment rates provided a better understanding of the effect of diversions relative to other sources of mortality. Satisfying these objectives comprehensively addressed factors affecting sauger abundances in the Yellowstone River and provided an understanding of sauger ecology under relatively pristine conditions. This understanding provides insight into factors affecting saugers throughout their range, as well as an enhanced comprehension of issues affecting migratory large-river fishes in general.

Study Area

The study area consisted of the lower 563 km of the Yellowstone River from near the Huntley Diversion, Montana, downstream to the river's confluence with the Missouri River in North Dakota (Figure 1). Mean annual (1929–2003) discharge at the U.S. Geological Survey gauging station in Miles City, Montana, was 323 m^3/s, mean annual peak discharge was 1,480 m^3/s, and mean annual low discharge was 71 m^3/s. River geomorphology varies throughout the study area in direct response to valley geology; straight, sinuous, braided, and irregular-meander channel patterns occur (Silverman and Tomlinsen 1984). The channel is often braided or split, and long side channels are common. Islands and bars range from large vegetated islands to unvegetated point and mid-channel bars (White and Bramblett 1993). Substrate is primarily gravel and cobble upstream of river kilometer (rkm) 50 (measured from the Missouri River confluence) and is primarily fines and sand downstream (Bramblett and White 2001). The fish assemblage is comprised of 49 species from 15 families, including eight state-listed species of special concern and one federally listed endangered species (White and Bramblett 1993; Carlson 2003). Water withdrawal for agriculture is the primary deleterious anthropogenic factor affecting the fish assemblage (White and Bramblett 1993). About 90% of all water use on the Yellowstone River is for irrigation, which corresponds to an annual usage of 1.8×10^9 m^3 (1.5 million acre-feet) (White and Bramblett 1993). Six main-stem low-head irrigation diversion dams occur in the study area (Figure 1). The largest and downstream-most of these, Intake Diversion, diverts about 38 m^3/s during the mid-May to mid-September irrigation season (Hiebert et al. 2000).

Methods

Seasonal distributions and movements.—Thirty or thirty-one saugers weighing 300–2,350 g were collected for telemetry by electrofishing or hook-and-line sampling each April from 2001 to 2003. Efforts were concentrated between Cartersville Diversion (rkm 379) and O'Fallon Creek (rkm 204; Figure 1) because declines in abundances were most marked in this reach and because saugers were no longer thought to occur above Cartersville Diversion (McMahon and Gardner 2001). In 2001, sampling efforts were focused on areas with seasonally high sauger abundances, as reported by previous studies. In 2002, about 1.6 out of every 16.1 km were sampled to minimize bias related to tagging location and to obtain a representative sample. In 2003, saugers were only collected directly downstream of the Powder and Tongue rivers to explicitly assess tributary use. Only sauger adults, as determined by lengths greater than 350 mm or the expression of gametes, were used (Haddix and Estes 1976; Carlander 1997). We used radio transmitters of two sizes to maximize battery life while avoiding transmitter-to-body-weight ratios in excess of 2% (Winter 1996). Small transmitters were 50 mm long and 10 mm in diameter, weighed 8.2 g, and had a minimum battery life of 300 d. Large transmitters were 50 mm long and 16 mm in diameter, weighed 14.3 g, and had a minimum battery life of 730 d. We used 24 small and 6 large transmitters in 2001; 20 small and 11 large transmitters in 2002; and only small transmitters in 2003. Radio transmitter frequencies ranged from 48.012 to 48.991 MHz, and each transmitter was equipped with a mortality sensor. Transmitters were implanted immediately after capture by use of procedures modified from Hart and Summerfelt (1975). Incisions were closed with size-35W stainless-steel surgical staples (Pegg et al. 1997). The 300-mm-long whip antennae trailed externally (Ross and Kleiner 1982). Transmitters were labeled with a return address and phone number to facilitate return by the public if fish were harvested or found dead. After surgery, saugers were placed briefly ($<$15 min) into a holding tank until they recovered from anesthesia and were released near the point of capture.

Saugers telemetered in 2001 and 2002 were relocated by boat once per week during April–June and twice per month during July–October. During November–March, when the river was ice covered, relocations were made by aircraft once during the winter of 2001–2002 and twice during the winter of 2002–2003. Saugers that were telemetered in 2003 were relocated weekly during April–June by boat or were judged to have moved into the Powder or Tongue rivers if recorded by permanent receiving stations near the mouths of these tributaries. The permanent receiving stations were deployed only in 2003. After detection, each sauger was located by triangulation and the coordinates of the location were determined by use of a hand-held global positioning unit (Winter 1996). Habitat type, channel position, and streambank characteristics at the point of relocation were recorded. Location was converted to river kilometer by means of geographical information system (GIS) software.

Annual patterns of movement between spawning and home locations were described by plotting relocation histories of telemetered saugers. Total and net movement rates (km/d) during each month were calculated for each telemetered sauger. The total movement rate was calculated by dividing the distance (km) between successive relocations of a given fish by the number of days that had elapsed between relocations (White and Garrott 1990). Net movement rate was calculated by dividing the change in river kilometer between successive relocations by the number of days that had elapsed between relocations, such that a positive rate indicated upstream movement and a negative rate indicated downstream movement (Bramblett 1996). Because additional movement may have occurred between relocations, calculated movement rates represent the minimum movement for the time period between relocations. Median monthly movement rates were compared by use of a Kruskal–Wallis test (Zar 1999). When significant differences were detected, Dunn's multiple comparison test was used to determine which monthly rates differed (Zar 1999).

Habitat use.—Seasonal habitat selection was examined at two hierarchically nested spatial scales: (1) reaches classified based on underlying geologic type and (2) pool–riffle-scale habitat types (Frissell et al. 1986). Geologic types were required to continuously span a minimum of 20 channel widths (about 4 km) to be considered a separate reach (Frissell et al. 1986; Leopold et al. 1992). Habitat types were classified as scour pool, bluff pool, terrace pool, valley bottom rip-rap scour pool, valley margin rip-rap scour pool, channel crossover, perennial secondary channel, or seasonal secondary channel. Scour pools were created by scour through valley bottom alluvium (Rabeni and Jacobson 1993). Bluff pools formed against bedrock at the valley margin (Rabeni and Jacobson 1993). We defined terrace pools as being adjacent to quaternary alluvial terrace deposits and colluvium. Valley bottom and valley margin rip-rap scour pools bordered rip-rap bank stabilization structures occurring in the valley bottom or at the valley margin, respectively. Channel crossovers occurred where the thalweg moved from one side of the channel to the other, as indicated by the presence of alternating depositional point bars. Perennial secondary channels were secondary channels that were clearly connected to the main channel at both ends and that continuously held water throughout their length at base flow. Seasonal secondary channels were not clearly connected to the main channel at both ends or did not continuously hold water throughout their length at base flow, but were likely to be fully connected during runoff.

Geologic reaches and habitat types were delineated on a ''habitat map'' created in ArcView GIS (ESRI 2002) based on information and GIS layers from 1:24,000-scale, low-level color infrared aerial photographs (Natural Resources Conservation Service 2002), a physical features inventory (Natural Resources Conservation Service 2002), and maps displaying underlying geologic type (Montana Bureau of Mines and Geology 1979, 1980, 1981a–1981b, 1998, 2000, 2001a–2001b). Thirteen reaches distributed among nine geologic types were delineated on the geologic maps between rkm 74 and 537, the range that encompassed the total observed distribution of telemetered saugers (Figure 1). Scour pools, channel crossovers, perennial secondary channels, and seasonal secondary channels were delineated based on the aerial photographs. Valley bottom and valley margin rip-rap pools were delineated from the physical features inventory. Bluff and terrace pools were delineated based on the geologic maps, which displayed where the channel scoured against bedrock or quaternary terrace material.

The availability of each geologic and habitat type during base flow and runoff periods was quantified with GIS software. The lengths of each geologic type reach and habitat unit were measured from delineations on the habitat map by use of the ArcView GIS 3.3 measure tool. Quantification was performed in a hierarchical manner such that the availability of each habitat type within a given geologic type was determined to allow for comparisons of selection among geologic types, habitat types, or habitat types stratified by geologic type. Availability at base flow was calculated by considering the amount of habitat provided by all habitat types except seasonal side channels. Availability during runoff included seasonal side channels.

Seasonal habitat use by saugers at both spatial scales was determined based on all telemetry relocations. Seasons were based empirically on sauger life history characteristics and movement rates. Seasons included spawning (March 15–May 15), postspawning movement (May 16–July 31), autumn (August 1–November 30), and winter (December 1–March 14). Spawning times and locations were verified by examination of female spawning condition (gravid, running eggs, or spent) during bi-weekly electrofishing surveys in geologic and habitat types occupied by telemetered saugers throughout the putative spawning period in 2003. The spawning season was bounded by the dates when the first spent female and the last gravid female were observed, and spawning locations were identified by the concurrent presence of female saugers that were gravid, running eggs, and spent. Habitat use by individual saugers was calculated for each season as the proportion of relocations that were made within each geologic type, habitat type, or habitat type stratified by geologic type (Manly et al. 2002). Use at both scales was determined from Global Positioning System coordinates of each relocation, field notes, color infrared aerial photographs, the physical features inventory (Natural Resources Conservation Service 2002), geologic maps (Montana Bureau of Mines and Geology 1979, 1980, 1981a–1981b, 1998, 2000, 2001a–2001b), and GIS software.

Chi-square tests with log-likelihood test statistics (Manly et al. 2002) were used to test the null hypothesis of seasonal selection in proportion to availability for different geologic types, habitat types, or habitat types stratified by geologic type. Although expected values were less than the commonly recommended minimum of 5 (Zar 1999), chi-square tests are robust to much smaller expected values (Roscoe and Byars 1971; Lawal and Upton 1984). Selection ratios and simultaneous 95% Bonferroni confidence intervals (Manly et al. 2002) were used to determine the level of selection for specific resource categories. Selection ratios for the population were obtained by averaging selection ratios calculated for individual telemetered saugers (Manly et al. 2002).

Aggregation.—Spatial distribution among individuals was examined for each week of telemetry relocations by use of a one-dimensional adaptation of neighbor K-statistics (O'Driscoll 1998). Analysis was performed with Matlab code provided by Richard O'Driscoll (National Institute of Water and Atmospheric Research, Kilbirnie, Wellington, New Zealand, personal communication). The statistical significance of spatial patterns was determined by including 90% confidence intervals of $L(t)$ (i.e., the number of neighbors observed beyond those that would be expected if saugers were randomly distributed at spatial scale t) obtained from 999 randomizations, which represented a significance level α of 0.10. Edge bias was not corrected for because the distribution and range of saugers in the sample were assumed to represent the complete distribution and range of the target population. Patch length was defined as the first distance t at which a maximal significant difference existed between the observed number of neighbors and the number of neighbors that would be expected if fish were randomly distributed; patch length represented the characteristic spatial scale of clustering. The height of the first peak in the plot of $L(t)$ represented a measure of the intensity of distribution, or degree of crowding. Crowding was defined as the difference between the observed and expected number of neighbors at the scale of the patch length and provided a measure of the number of individuals that were grouped together in a patch. Spatial relationships were plotted continuously over the study period by use of an unpublished clustering index developed by Richard O'Driscoll. The index was calculated at each distance t by dividing (1) the average number of individuals within t for any given individual in the distribution of telemetered saugers by (2) the mean of the same values for each of the randomizations.

Exploitation.—Exploitation was examined by assessment of tagged fish recaptured by anglers. A total of 199 saugers in 2001, 332 saugers in 2002, and 295 saugers in 2003 were tagged between Cartersville Diversion (rkm 379) and Intake Diversion (rkm 115). Saugers were captured by electrofishing or hook-and-line sampling. Tagging occurred during the spawning and autumn seasons; 62–84% of the tagging in a given year occurred during the spawning season. To minimize bias related to the lengthy tagging season, we maintained a similar median week of tagging during each year of the study (Smith et al. 2000). To determine whether the tagging regime resulted in biased estimates of annual survival or exploitation, a simulation program was designed to generate data sets from a virtual population subjected to monthly rates of tagging, natural mortality, and fishing mortality that were similar those experienced by the lower Yellowstone River sauger population. Bias was assessed by (1) estimating survival and exploitation for 100 generated data sets with the methods used to estimate these parameters for the study population and (2) comparing calculated mean annual survival and exploitation rates to the known values for the virtual population. Sampling and tagging occurred in the same locations as described for telemetered fish during the spawning season and in four 8.05-km (5 mi) sections located near Cartersville Diversion and the confluences of the Tongue River, Powder River, and O'Fallon Creek during the autumn season. Saugers were tagged by the authors, Montana Fish, Wildlife and Parks biologists and technicians, or an angler trained in correct tagging techniques. Each sauger received two individually numbered Floy FD-94 T-bar tags inserted below the spiny and soft dorsal fins about 1 cm apart. Tags were marked ''REWARD'' and included a telephone number to report recovery of tagged fish. Tagged saugers were released immediately after tagging near the point of capture.

Angler return of tagged fish was solicited by placing signs describing the project and providing postage-paid envelopes with attached tag return forms at fishing access sites along the Yellowstone River. Newspaper and radio advertisements and press releases describing the project and procedures for returning tag recovery information were disseminated. Reward caps (MacRitchie and Armstrong 1984) were mailed to anglers returning tags to attempt to enhance tag return rates. Anglers were asked to provide their name, address, and phone number and the following information for each tagged sauger recovered: date and location of fish capture or discovery, fish length and weight, whether the fish was kept or released, the number of tags recovered, and tag numbers. Anglers were able to return tags by mail, phone, or in person at the Montana Department of Fish, Wildlife and Parks regional offices in Miles City and Billings.

Annual survival and annual and seasonal probabilities of capture and exploitation were estimated by analysis of T-bar tag returns based on recovery models described by Brownie et al. (1985). Candidate models allowing survival, probability of capture, and probability of exploitation to remain constant or vary through time were constructed and parameterized in the program MARK (White and Burnham 1999; Cooch and White 2001). To allow direct comparison of sauger movement and aggregation patterns, seasons were defined as spawning movement (March 15–July 31), autumn (August 1–November 30), and winter (December 1–March 14). Seasonal survival could not be calculated from T-bar tag returns because no detectable fishing occurred during winter. Survival and probability of capture were estimated based on the tag returns of all captured fish during a given period. Exploitation was estimated only from tag returns of harvested fish. Goodness-of-fit testing was performed for each set of candidate models by use of the most general model and the program ESTIMATE (Cooch and White 2001). The overdispersion parameter, $\hat{c}$, was calculated to assess lack of fit (Cooch and White 2001). If $\hat{c}$ was greater than 1, models were adjusted to correct for overdispersion. We used MARK to obtain parameter and variance estimates for all parameters other than nonfishing mortality by model averaging based on Akaike's information criterion (AIC) values corrected for small-sample bias (AIC_c) and, when applicable, overdispersion (QAIC_c) (Burnham and Anderson 1998; Cooch and White 2001). Variance estimates for nonfishing mortality were obtained by use of the delta method (Seber 1982). Survival estimates were adjusted for bias resulting from angler release of saugers after tag removal (Smith et al. 2000).

Prior to analysis, tag returns from captured or harvested saugers were adjusted for tag loss and nonreporting. Each sauger was double tagged, and tag loss was estimated by use of the tag shedding model, $Q(t) = (1 - \rho)e^{(-Lt)}$, where $Q(t)$ is the probability of a tag being retained at time t after release, ρ is the immediate type-I shedding rate, and L is the continuous type-II shedding rate (Hampton 1997). Maximum likelihood estimates of ρ and daily L were obtained by minimizing the probability density function described by Hampton (1997). Tag returns were adjusted for tag loss in each year or season by dividing the number of observed tag returns from a given period by $1 - P_0(t)$, where $P_0(t)$ is the probability of zero tag retention at time t after release and is equal to $[1 - Q(t)]^2$ (Hampton 1997). The time interval t was the total length of the fishing period in days. Its use resulted in maximum estimates of tag loss because captured fish were not at large for the entire fishing year or season in which they were captured. Nonreporting of tagged fish was estimated based on postcards used as tag surrogates (Zale and Bain 1994). Nonreporting was adjusted for by multiplying the number of fish tagged during each fishing period by the reporting rate observed for the tag surrogates (Seber 1982).

Independent estimates of annual and seasonal survival rates were calculated with data from telemetered fish. To be considered to have survived the period of interest, telemetered saugers were required to have been located alive at the end of that period. Saugers with transmitters that emitted mortality signals, saugers that were reported as harvested, and saugers that were not located after a given season were considered to have died during the period of interest. Possible fates other than mortality for unrelocated saugers included emigration from the study area and transmitter failure (Seber 1982). Prior to estimation, encounter histories were adjusted for transmitter failure. The rate of transmitter failure was reported to be 10% over the lifetime of the transmitter (Dick Richle, Advanced Telemetry Systems, Isanti, Minnesota, personal communication); as a result, one unrelocated fish per season or three unrelocated fish per year were not counted as mortalities. Although we were not able to obtain emigration estimates, we searched well beyond the boundaries of the observed spatial distribution of telemetered saugers, and therefore we suspect that emigration was low. However, because a possibility exists that unrelocated saugers may have emigrated from the study area and survived, the estimates obtained should be considered to represent ‘‘apparent survival’’ and may be equal to or less than true survival. Parameter estimates and 95% confidence intervals were obtained from model averaging and AIC$_c$ weights of known-fate candidate models by use of MARK (Burnham and Anderson 1998; Cooch and White 2001).

Entrainment.—The number of saugers tagged in the Yellowstone River and entrained in Intake Diversion Canal was estimated by dividing (1) the number of saugers tagged in the Yellowstone River and captured by anglers in Intake Diversion Canal by (2) the exploitation rate of ‘‘canal-resident’’ saugers. Canal residents were those saugers tagged in Intake Diversion Canal (71 in 2001; 60 in 2002) after entrainment. The exploitation rate was calculated by dividing (1) the number of canal-resident saugers captured by anglers by (2) the number of tagged canal-resident saugers (Ricker 1975). Tag loss and nonreporting were adjusted for as described above. An approximation of the annual probability of entrainment was calculated by dividing (1) the estimated number of saugers tagged in the Yellowstone River and entrained in Intake Diversion Canal by (2) the number of saugers tagged in the Yellowstone River.

Results

Seasonal Distributions and Movements

The observed annual movement pattern consisted of downstream movements to spawning areas during March–May followed by return movements to upstream home river locations during April–July (Figure 2). In 2003, the first observation of female saugers freely expelling eggs occurred on April 18, spent females were first collected on April 24, and gravid females were last collected on May 1. Spawning locations were distributed over a distance of 116–146 km and occurred from the confluence with the Tongue River to about 60 km downstream of Intake Diversion (Figure 1). Home locations were distributed over a distance of 200–325 km and occurred from about 20 km above Waco Diversion to the confluence with the Powder River (Figure 1). Home and spawning locations of individual fish were spatially distinct; the round-trip distance of the annual migration between spawning and home river locations ranged from 10 to 600 km and averaged 89.5 km. Average fidelity to spawning locations (4.7 km) and home river locations (0.0 km) was high for fish relocated over a complete migration cycle; all saugers reoccupied individual home location habitat units, and 8 of the 11 saugers relocated during consecutive spawning periods used the same individual habitat unit that was used during the previous year. Use of tributaries for spawning by telemetered saugers was rare; one fish used the Powder River (3.3%) during the spawning season in 2003, and no fish used the Tongue River.

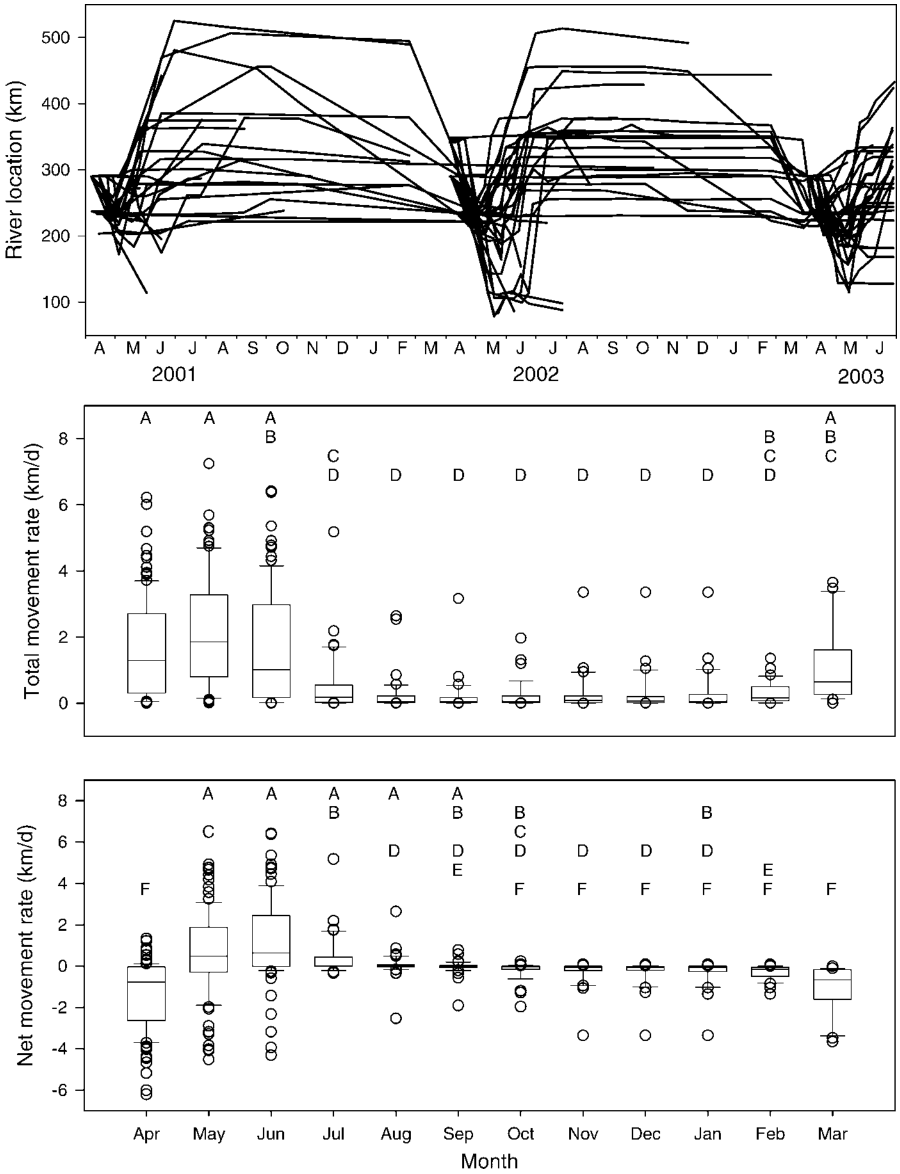

FIGURE 2.—Movement patterns of telemetered saugers in the Yellowstone River during 2001–2003. In the top panel, lines represent individual telemetered saugers and river location describes the distance from the confluence with the Missouri River. In the middle panel, total movement rates are shown by month; the lines within the boxes represent medians, the vertical boundaries of the boxes represent 25th and 75th percentiles, the whiskers represent 10th and 90th percentiles, and the circles represent outliers beyond the 10th and 90th percentiles. Movement rates for months with the same letters are not significantly different among months or years ($P \geq 0.05$). In the bottom panel, net movement rates are shown by month; lines, boxes, whiskers, and circles are the same as described above. Negative values indicate predominately downstream movements, positive values indicate predominately upstream movements, and values near zero indicate no directionality of movement. Net movement rates for months with the same letters are not significantly different among months or years ($P \geq 0.05$).

Total movement rates of saugers varied among months ($P < 0.001$; Figure 2) but were the same among years during specific months. Total movement rates were high during February–June (median = 1.00 km/d) and were not significantly different during these months within or among years. Net movement rates of saugers varied among months ($P < 0.001$; Figure 2) but were the same among years during specific months. In all years, net movement rates in June indicated predominately upstream movement and were significantly different than those observed in March and April, which indicated predominately downstream movement. Movements were nondirectional during all other months of the year.

We observed sauger movements past all dams except Huntley Diversion. Consecutive relocations immediately below dams were rare, indicating the absence of passage delays. However, at least one telemetered sauger was relocated immediately below Cartersville Diversion during autumn of each year, and such fish may have been prevented from moving past this structure. Conversely, saugers may have simply selected this habitat. Saugers with home locations upstream of Cartersville Diversion were significantly longer than those with downstream home locations (t-test, $P = 0.048$), but saugers as small as 385 mm successfully passed this dam. Spawning and home locations of most telemetered saugers (80%) were situated between the Cartersville and Intake diversions, such that no dams were encountered during migrations.

Habitat Use

Saugers did not use habitat resource categories in proportion to their availability ($P \leq 0.05$) except for winter habitat types and movement season habitat types nested within geologic types. Saugers demonstrated positive selection for the Tullock and Lebo members of the Fort Union Formation and avoided all other geologic types during spawning (Figure 3). Bluff and terrace pools were positively selected during the spawning season, and all other habitat types were avoided (Figure 3). However, terrace pools were used in proportion to their availability within half of the geologic types that were avoided (Figure 4). In 2003, female saugers that were gravid, running eggs, and spent were simultaneously observed only in selected habitat and geologic types.

Selection of geologic type during the movement season was intermediate between selection during the spawning and autumn seasons (Figure 3). Habitat types were used in proportion to their availability during the movement season except for terrace pools, which were positively selected, and secondary channels, which were negatively selected (Figure 3). However, secondary channels were the most commonly used habitat type during the movement season, and negative selection resulted from their high availability throughout the study area during runoff. Within geologic types, saugers used habitat types in proportion to their availability during the movement season (Figure 4).

Saugers selected specific geologic types during autumn (Figure 3) while demonstrating no selection for habitat types except terrace and valley bottom rip-rap pools, which were avoided (Figure 3). Most habitat types within the Tullock Member of the Fort Union Formation and the Lance and Hell Creek formations were used in proportion to their availability, whereas most habitat types within all other geologic types were avoided (Figure 4).

During winter, saugers continued to select specific geologic types (Figure 3) while using habitat types in proportion to their overall availability. Within geologic types, scour and bluff pools were the most consistently used habitat types, although rip-rap valley margin pools were used most frequently overall (Figure 4).

Aggregation

Across their entire observed spatial distribution, saugers were significantly aggregated only during a 2–3-week period associated with spawning in late April and early May (Figure 5a, f). Patch length ranged from 3 to 6 km during this time, and the crowding index within a patch indicated that there were about two to three times as many telemetered saugers as would be expected if spatial associations were random. Aggregation was greatest during the week of peak spawning each year, when 28–36% of the telemetered saugers were relocated within 6 km of the Powder River confluence. During the period of upstream movement that occurred after spawning, the intensity of aggregation began to decrease and an intermediate pattern of spatial association was observed at most scales (Figure 5b). Saugers exhibited significant random distributions at all spatial scales during the late-summer, autumn (Figure 5c), and winter (Figure 5d) sedentary periods and during the period of downstream movement in early spring (Figure 5e). Significant aggregation at most spatial scales began to occur again during April in association with spawning (Figure 5f). This seasonal

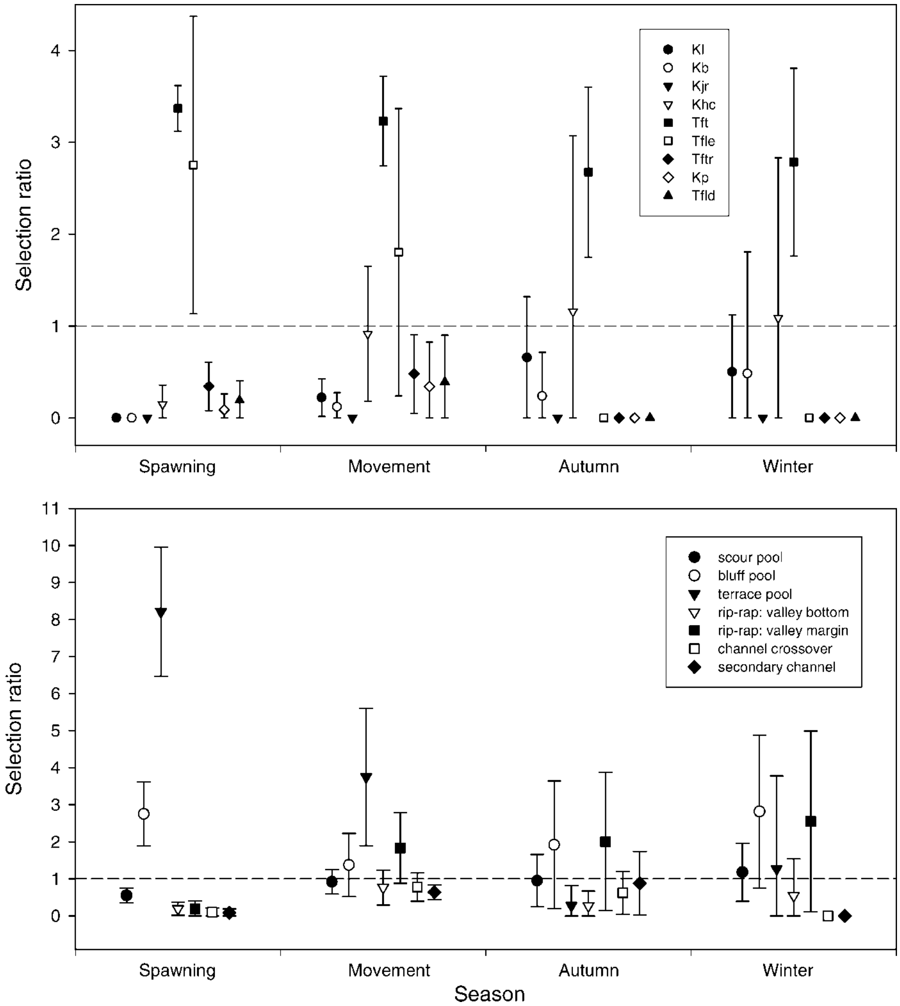

FIGURE 3.—Seasonal selection of geologic types and habitat units by telemetered saugers in the Yellowstone River, 2001–2003. Selection ratios larger than 1 indicate positive selection, values equal to 1 indicate use in proportion to availability, and values less than 1 indicate negative selection. Error bars represent simultaneous 95% Bonferroni confidence intervals. Geologic types are Lance Formation (Kl), Bearpaw Shale (Kbp), Judith River Formation (Kjr), Hell Creek Formation (Khc), Tullock Member of the Fort Union Formation (Tft), Lebo Member of the Fort Union Formation (Tfle), Tongue River Member of the Fort Union Formation (Tftr), Pierre Shale (Kp), and Ludlow Member of the Fort Union Formation (Tfld).

pattern of spatial association occurred during all years of the study (Figure 6).

Exploitation

The probability of immediate tag shedding was 0.04115, the instantaneous daily probability of continuous tag shedding was 0.00031, and the tag reporting probability was 0.385. Brownie et al. (1985) models were robust to the tagging regime used in this study; simulations indicated that the methods we used resulted in unbiased survival and exploitation estimates on average. The most general model from each group of candidate models adequately fit the data based on goodness-of-fit testing ($P \geq 0.05$). Overdispersion was detected in the models used to estimate annual exploitation and was adjusted for accordingly.

The annual probability of survival, estimated from T-bar tag data, was 0.726 in 2001 and 0.682 in 2002; the annual probability of apparent survival, estimated from telemetry data, was 0.519 in 2001 and 0.516 in 2002 (Table 1). The annual cap-

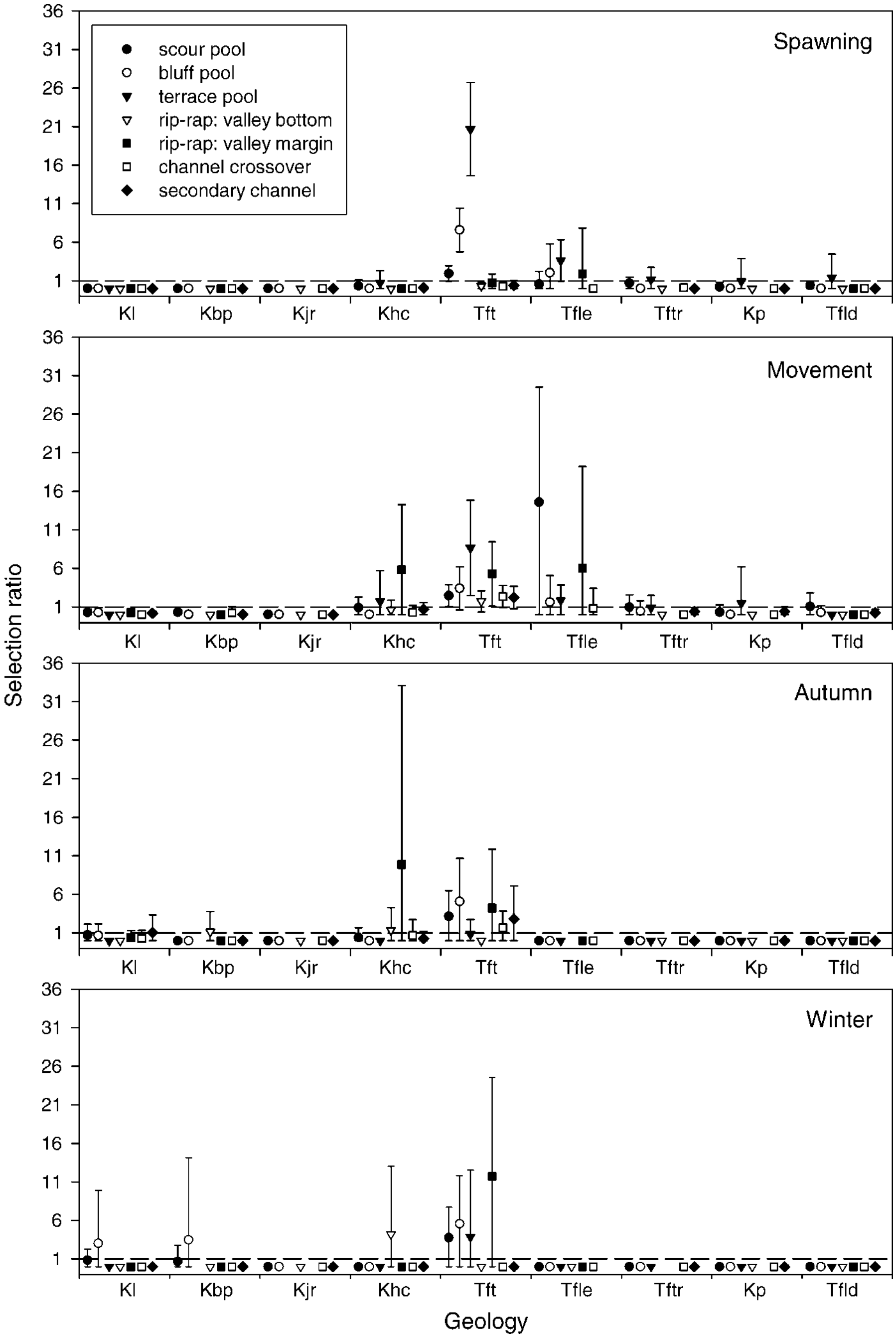

FIGURE 4.—Seasonal selection by telemetered saugers in the Yellowstone River of habitat units stratified by geologic type, 2001–2003. Selection ratios larger than 1 indicate positive selection, values equal to 1 indicate use in proportion to availability, and values less than 1 indicate negative selection. Error bars represent simultaneous 95% Bonferroni confidence intervals. Geologic types are Lance Formation (Kl), Bearpaw Shale (Kbp), Judith River Formation (Kjr), Hell Creek Formation (Khc), Tullock Member of the Fort Union Formation (Tft), Lebo Member of the Fort Union Formation (Tfle), Tongue River Member of the Fort Union Formation (Tftr), Pierre Shale (Kp), and Ludlow Member of the Fort Union Formation (Tfld).

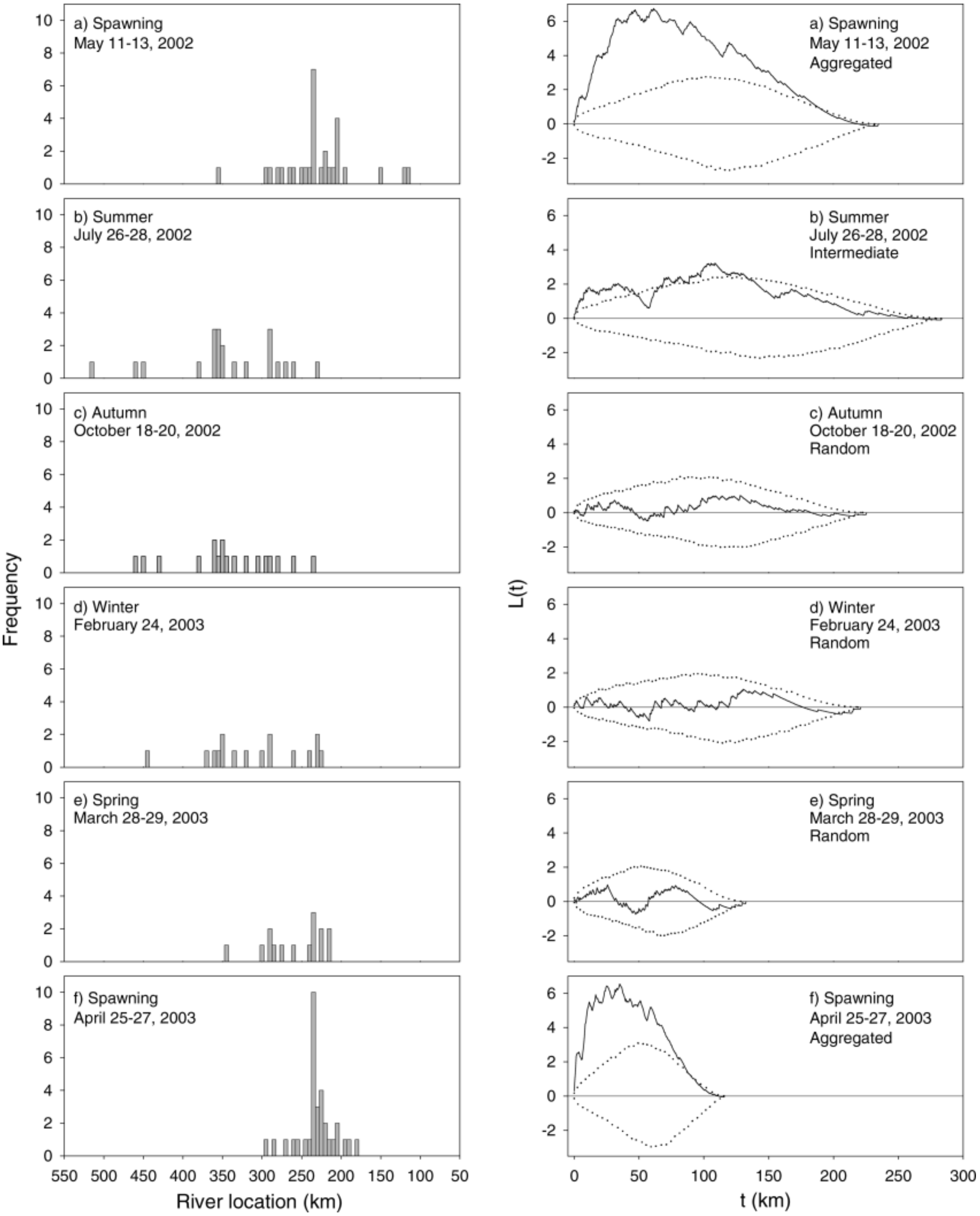

FIGURE 5.—Selected examples of seasonal variation in the distribution (left) and spatial association (right) of saugers telemetered in the lower Yellowstone River. River location describes the distance from the confluence with the Missouri River. On the spatial association plots, the solid line $L(t)$ represents the number of neighbors observed beyond those that would be expected if saugers were randomly distributed at spatial scale t. The distribution is significantly aggregated ($P \leq 0.10$) at spatial scale t when $L(t)$ is above the upper 90% confidence band shown by the dashed lines.

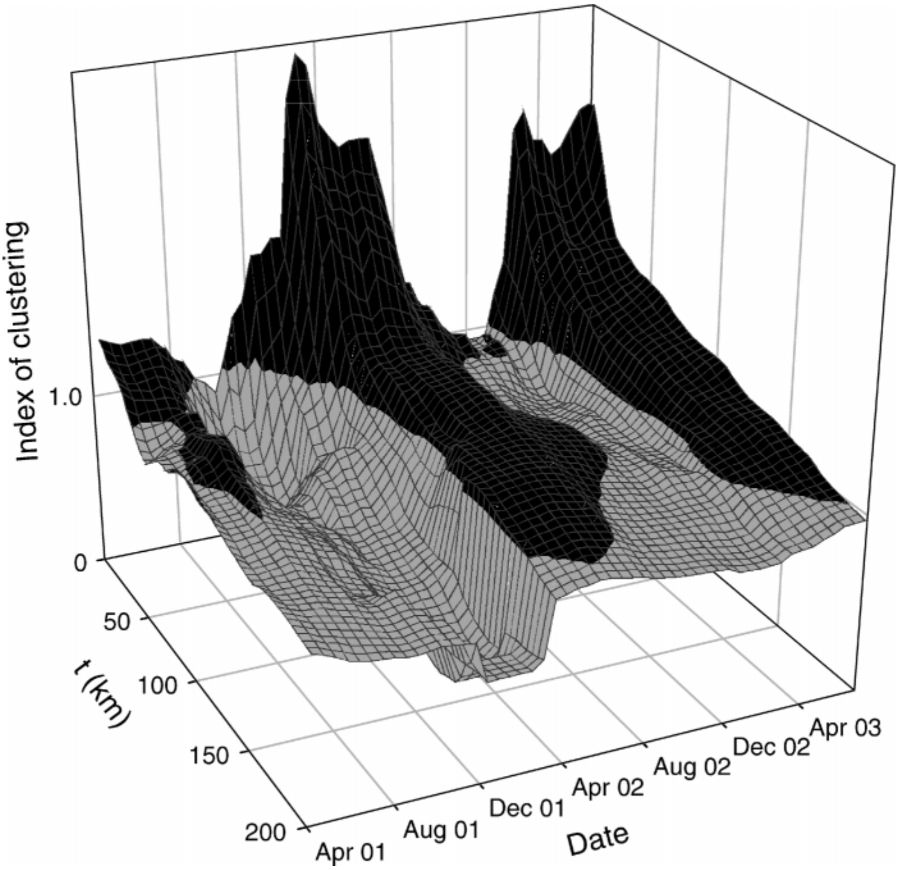

FIGURE 6.—Clustering index for telemetered saugers in the lower Yellowstone River, 2001–2003. For a given spatial scale *t*, values greater than 1 (black) indicate aggregated distribution and values less than 1 (gray) indicate random distribution.

ture probability ranged from 0.300 to 0.323, and the annual exploitation probability ranged from 0.159 to 0.201 (Table 1).

Apparent seasonal survival probabilities during 2001 and 2002 were 0.804 and 0.782 during the spawning movement period, 0.801 and 0.817 during autumn, and 0.816 and 0.810 during winter (Table 1). During the spawning-movement period, the capture probability ranged from 0.048 to 0.154 and the exploitation probability ranged from 0.013 to 0.044 (Table 1). During autumn, the capture probability ranged from 0.237 to 0.772 and the exploitation probability increased from 0.145 in 2001 to 0.387 in 2003 (Table 1). Most of the mortality that occurred during the spawning-movement period appeared to be related to nonfishing sources, whereas almost all of the mortality that occurred during autumn was related to exploitation (Table 1).

Entrainment

The exploitation probability for canal-resident saugers was 0.741 in 2001 and 0.435 in 2002. The estimated number of tagged saugers that were entrained in Intake Diversion Canal was 5 in 2001 and 12 in 2002. The annual probability of entrainment in Intake Diversion Canal was 0.065 in 2001 and 0.094 in 2002. These rates represented 56.5% and 78.3% of the estimated annual nonfishing mortality in 2001 and 2002.

Discussion

Movement patterns of Yellowstone River saugers differed from patterns displayed by saugers in impounded systems. For example, annual migrations between spawning and home areas in the Yellowstone River were among the longest reported, but impoundments precluded similar

TABLE 1.—Annual and seasonal estimates of sauger survival, exploitation, and mortality in the lower Yellowstone River, 2001–2003. Probability of apparent survival ($\Phi_{\text{telemetry}}$) was estimated based on known-fate models and data from telemetered saugers. The probability of survival ($S_{\text{T-tag}}$), probability of capture (f), probability of harvest (u), and expectation of nonfishing mortality (v) were estimated by use of Brownie et al. (1985) models and data from T-bar-tagged saugers. Confidence intervals (95%) for parameter estimates are shown in parentheses.

Year and season	$\Phi_{\text{telemetry}}$	$S_{\text{T-tag}}$	f	u	v
2001	0.519	0.726	0.300	0.159	0.115
	(0.336, 0.696)	(0.529, 0.925)	(0.237, 0.372)	(0.072, 0.318)	(0.000, 0.310)
Spawning movement	0.804		0.154	0.031	0.165
	(0.682, 0.887)		(0.085, 0.263)	(0.008, 0.114)	(0.059, 0.271)
Autumn	0.801		0.772	0.145	0.054
	(0.672, 0.888)		(0.056, 0.995)	(0.052, 0.341)	(0.000, 0.162)
Winter	0.816		0.00	0.00	0.184
	(0.679, 0.903)				(0.087, 0.280)
2002	0.516	0.682	0.302	0.198	0.120
	(0.345, 0.683)	(0.492, 0.871)	(0.247, 0.364)	(0.123, 0.303)	(0.000, 0.300)
Spawning movement	0.782		0.114	0.044	0.174
	(0.642, 0.878)		(0.066, 0.189)	(0.019, 0.103)	(0.073, 0.274)
Autumn	0.817		0.237	0.195	0.000
	(0.674, 0.906)		(0.177, 0.310)	(0.137, 0.269)	(0.000, 0.112)
Winter	0.810		0.00	0.00	0.190
	(0.672, 0.899)				(0.098, 0.282)
2003			0.323	0.201	
			(0.256, 0.398)	(0.123, 0.311)	
Spawning movement			0.048	0.013	
			(0.027, 0.085)	(0.004, 0.040)	
Autumn			0.628	0.387	
			(0.476, 0.758)	(0.248, 0.546)	
Winter			0.00	0.00	

movement distances in other systems (Nelson 1968; St. John 1990; Hesse 1994; Pegg et al. 1997). Downstream migration to spawning areas was also unique to the Yellowstone River, whereas only upstream migrations to riverine habitats are possible elsewhere (Nelson 1969; St. John 1990; Pegg et al. 1997). The timing of migration also differed. Saugers in the Yellowstone River migrated to spawning areas in spring after overwintering in the same areas used during summer and autumn. Two-stage migrations were reported for dam-influenced populations; saugers moved out of reservoirs in autumn and overwintered in tailwaters below dams before moving to nearby spawning areas in spring (Nelson 1968; St. John 1990; Pegg et al. 1997). Accordingly, lotic habitats may be preferred during winter, especially where hypolimnetic discharges afford favorable conditions (Marcy and Galvin 1973; Crance 1988). Conversely, harsh winter conditions (spring ice flows and ice jams near spawning areas; Cunjak 1996) in the Yellowstone drainage at the western edge and altitudinal extremes of sauger distribution (Scott and Crossman 1973; White and Bramblett 1993) may delay migration until spring. Fidelity to spawning and home locations is common for walleyes *S. vitreus* (Olson et al. 1978) but was previously not described for saugers.

Contrary to what has been previously hypothesized, diversion dams did not appear to restrict the movements of adult saugers (Graham et al. 1979; Swedberg 1985; Helfrich et al. 1999; McMahon and Gardner 2001). Upstream movements coinciding with periods of high discharge probably facilitated passage beyond dams; movements at other times of the year, when discharge was low and when dam passage may have been hindered, were rare. The presence of large saugers upstream of Cartersville Diversion suggests that ascension past the barrier was size dependent. However, relatively small saugers were observed passing this dam; larger saugers may simply migrate further on average. Although we observed no movements past Huntley Diversion, this barrier was beyond the distribution of the telemetered saugers and was probably not encountered by the fish. The failure of most saugers to encounter dams during migrations between spawning and home locations may be an artifact of tagging locations; all saugers were telemetered between the Cartersville and Intake diversions, at least 40 km from the nearest dam. Whereas the effects of these dams on adult sauger passage are perhaps ambiguous, clear evidence of restricted upstream movement of juveniles exists. The sauger catch rate downstream of Intake Diversion was about 23 fish/h, whereas the catch rate from O'Fallon Creek to the Big Horn River was about 4 fish/h (Jaeger 2005). Most fish captured downstream of Intake Diversion were juveniles, whereas most fish captured upstream were adults (Penkal 1992; Jaeger 2005).

Home river locations were most strongly influenced by geologic type. Selected reaches (Tullock Member and Lance and Hell Creek formations) were comprised of relatively resistant sandstone, and avoided reaches (Bearpaw Shale) were comprised of softer and more erosive shales (Montana Bureau of Mines and Geology 1979, 1980, 1981a–1981b, 1998, 2000, 2001a–2001b; Boyd and Thatcher 2004). The differences in resistance among geologic types result in a strong relationship between geologic type and valley configuration; the presence of shale rather than sandstone correlates to an abrupt widening of the valley bottom (Boyd and Thatcher 2004). Selected geologic types had irregular valleys that were narrower and more resistant and that exhibited more control on channel margins than did avoided reaches (Silverman and Tomlinsen 1984). Although no comprehensive geomorphic assessments of the Yellowstone River exist (Boyd and Thatcher 2004), differences in geomorphology can be inferred based on the relative resistance of geologic types. Resistant sandstones probably maintained an asymmetric channel cross section with deep, vertical cut banks, leaving little impetus for the channel to migrate and allowing formation of deep, long pools (K. Boyd, Applied Geomorphology, Inc., Bozeman, Montana, personal communication). Valley margins in Bearpaw Shale reaches, which were avoided, tended to slope back and fail as river meanders migrated into them, probably resulting in a higher width-to-depth ratio, lower velocity, lower depth, and a more-braided channel pattern in these reaches (K. Boyd, personal communication). Geologic types used for spawning were probably not used for home locations because of low complexity. Spawning areas were dominated by bluff and terrace pools, whereas the most heavily used home location geologic types had higher habitat diversity and complexity.

Saugers spawned in more locations than have previously been reported, and spawning habitat did not appear to be limited. Heretofore, spawning habitat was thought to be scarce; only three discrete spawning areas had been documented (Penkal 1992), and one of these (the Tongue River) is no longer used because of chronic dewatering (McMahon and Gardner 2001). However, telemetered saugers used many spawning areas from the Tongue River confluence to below Intake Diversion. The most concentrated spawning activity occurred between the Powder River and O'Fallon Creek. Ostensibly, suitable spawning habitats were not rare, although they were confined to discrete reaches of stream.

The presence of boulder and bedrock substrates influenced selection of habitats during spawning. Bluff and terrace pool habitats, which recruit boulder-sized substrate from hill slopes (Rabeni and Jacobson 1993), were selected by saugers; all other habitat types were avoided. Spawning aggregation patch length was consistent with bluff and terrace pool length. Geologic types characterized by reef-forming bedrock outcrops (Silverman and Tomlinsen 1984) were also used. Sauger spawning is often associated with large, rocky substrates and bedrock reefs (Nelson 1968; Gardner and Stewart 1987; St. John 1990; Hesse 1994) and turbid, warm tributaries (B. Graeb, South Dakota State University, Brookings, personal communication); most spawning in the Yellowstone River occurred downstream of the Powder River, which is a major source of turbidity (Rehwinkel 1978).

Telemetered saugers spawned almost exclusively in main-stem habitats, whereas previous studies suggested that most spawning occurred in tributaries (Penkal 1992; McMahon and Gardner 2001). Rare tributary use was consistent with previously reported declines (McMahon and Gardner 2001) and low electrofishing catch rates in the Tongue and Powder rivers in 2003 (M. Backes, Montana Fish, Wildlife and Parks, Miles City, personal communication). Mean April discharge in the Tongue River was well below minimum sauger spawning and passage requirements (Elser et al. 1977) during each year of the study. However, better conditions occurred in the Powder River; mean April discharge was about 70% of the 66-year average in 2003. The failure of saugers to use the Powder River despite improved discharge may be influenced by learned homing behavior (Olson et al. 1978); disruption of tributary spawning during drought conditions may have resulted in failure to transfer tributary migration behavior to younger age-classes. Higher discharge levels than those observed during this study may be required for tributary spawning.

The aggregation behavior of Yellowstone River saugers differed from that of populations occurring in impounded systems. Fewer aggregations were observed in other systems (Nelson 1968; Gardner and Stewart 1987; St. John 1990; Pegg et al. 1997) than in the Yellowstone River. The large number and wide distribution of sauger spawning aggregations in the Yellowstone River may represent natural spatial patterns in the absence of main-stem impoundments, which restrict movements to some degree in the other systems. Saugers in the Yellowstone River were aggregated for a shorter duration than those in other systems. Aggregations resulting from impeded autumn and winter migrations caused by main-stem impoundments occurred as early as November elsewhere (Nelson 1968; Pegg et al. 1997). Aggregations formed later in the Yellowstone River because of relatively late migrations (March–April) to spawning areas and did not occur at diversion dams because passage was apparently unrestricted in those areas.

Exploitation of spawning aggregations was less pronounced in the Yellowstone River than in impounded systems. Most harvest in overexploited sauger populations occurs during extended periods of aggregation (Pegg et al. 1996; Maceina et al. 1998); however, Yellowstone River exploitation rates were lower during the spawning-movement aggregation season (1–4%) than in autumn (14–39%), when saugers were randomly distributed. Although anglers targeted primary areas of aggregation, the relatively short duration and large number of aggregations may have reduced the risk of overexploitation.

Harvest by anglers probably does not prevent recovery of the Yellowstone River sauger population. Relatively low exploitation (15–20%) and high survival (68–73%) rates were observed. High survival rates were corroborated by the length-determined age structure of saugers collected for this study; about half of the tagged fish were 5–10 years old (Haddix and Estes 1976; Carlander 1997). High proportions of old fish are characteristic of lightly exploited stocks (Van Den Avyle and Hayward 1999). Elsewhere, sauger populations declined or collapsed when exploitation rates were 30–90% and survival rates were less than 30%; these populations were comprised almost exclusively of age-1 and age-2 individuals (Pegg et al. 1996; Maceina et al. 1998).

Although exploitation rates were relatively low, the potential exists for high exploitation of Yellowstone River saugers. Annual exploitation would increase to over 30% if all captured saugers were harvested. This effect is most pronounced in autumn; the capture rate was high (24–77%), but voluntary release (37%) reduced exploitation rates. High autumn capture (63%) and exploitation (39%) rates in 2003 may have been biased given the low annual exploitation rate (20%); an increase in the angler reporting rate occurring late in the study may have accounted for the high seasonal capture and exploitation rates observed. Potential for high exploitation also exists at the Powder River aggregation because of its comparatively large size and popularity among anglers.

Entrainment in Intake Diversion Canal was an important source of nonfishing mortality. Most mortality that occurred during the spawning movement period was related to nonfishing sources, and as much as half was related to entrainment in Intake Diversion Canal. It is likely that entrainment occurs to some degree at the other five diversion dams, potentially making it the primary source of nonfishing mortality in adult saugers. Furthermore, most entrained saugers were less than 3 years old (Hiebert et al. 2000), such that juveniles probably experience higher entrainment-caused mortality rates than adults.

Although the primary factors delaying the return of Yellowstone River saugers to historical abundances remain unclear, reducing mortality rates may increase abundances. Elimination of entrainment is likely to be a more effective restorative action than angler harvest restrictions. The high survival rates and additive mortality observed for adult saugers suggest that increased juvenile survival and recruitment will result in increased adult abundances. Although eliminating entrainment in irrigation diversions may reduce annual mortality of adult saugers by at least 24–30%, even larger reductions in juvenile mortality rates are likely, as most entrained saugers are juveniles (Hiebert et al. 2000). Abundances of adult saugers would be bolstered by reduced mortality combined with increased juvenile recruitment. If anglers are allowed to continue harvesting saugers, they will remain concerned about the status of the population, thereby providing important cultural and political motivation for sauger recovery.

Sauger ecology under relatively pristine and unimpounded conditions differed from that occurring in more altered systems. Consistent with paradigms for riverine fishes (i.e., Schlosser 1991; Fausch et al. 2002), our study indicates that unrestricted saugers exhibited large annual movements among a wide variety of spatially distinct and diverse habitats. Saugers in impounded systems exhibited shorter movements, fewer and larger aggregations, and restricted use of altered or simplified habitats (Nelson 1968; St. John 1990; Hesse 1994; Pegg et al. 1997). The restoration of passage and natural riverine function to fragmented systems will facilitate movements between spatially distinct, diverse spawning and home locations and will reduce the risk of overexploitation by allowing natural patterns of aggregation to occur.

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References

Amadio, C. J., W. A. Hubert, K. Johnson, D. Oberlie, and D. Dufek. 2005. Factors affecting the occurrence of saugers in small, high-elevation rivers near the western edge of the species' natural distribution. Transactions of the American Fisheries Society 134: 160–171.

Boyd, K. F., and T. Thatcher. 2004. Geomorphic reconnaissance and GIS development Yellowstone River, Montana. Applied Geomorphology, Inc., Report to Custer County Conservation District, Miles City, Montana.

Bramblett, R. G. 1996. Habitats and movements of pallid and shovelnose sturgeon in the Yellowstone and Missouri rivers, Montana and North Dakota. Doctoral dissertation. Montana State University, Bozeman.

Bramblett, R. G., and R. G. White. 2001. Habitat use and movements of pallid and shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota. Transactions of the American Fisheries Society 130:1006–1025.

Brownie, C., D. R. Anderson, K. P. Burnham, and D. S. Robson. 1985. Statistical inference from band recovery data: a handbook. U.S. Fish and Wildlife Service Resource Publication 156.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference. Springer-Verlag, New York.

Carlander, K. D. 1997. Handbook of freshwater fishery biology, volume 3. Life history data on ichthyopercid and percid fishes of the United States and Canada. Iowa State University Press, Ames.

Carlson, J. 2003. Montana animal species of special concern. Montana Natural Heritage Program and Montana Fish, Wildlife and Parks, Helena.

Collette, B. B., M. A. Ali, K. E. F. Hokanson, M. Nagiec, S. A. Smirnov, J. E. Thorpe, A. H. Weatherley, and J. Willemsen. 1977. Biology of the percids. Journal of the Fisheries Research Board of Canada 34: 1890–1899.

Cooch, E., and G. C. White. 2001. Program MARK: a gentle introduction. Available: www.phidot.org/software/mark/docs/book/. (April 2004).

Crance, J. H. 1988. Preliminary habitat suitability curves for sauger. Proceedings of the Annual Conference Southeastern Association Fish and Wildlife Agencies 41(1987):159–167.

Cunjak, R. A. 1996. Winter habitat of selected stream fishes and potential impacts from land-use activity. Canadian Journal of Fisheries and Aquatic Sciences 53(Supplement 1):267–282.

Elser, A. A., R. C. McFarland, and D. Schwehr. 1977. The effects of altered streamflows on the fish of the Yellowstone and Tongue rivers, Montana. Montana Department of Natural Resources and Conservation, Technical Report 8, Yellowstone Impact Study, Helena.

ESRI. 2002. ArcView GIS, version 3.3. ESRI, Redlands, California.

Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52:1–16.

Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10:199–214.

Gardner, W. M., and R. K. Berg. 1980. An analysis of the instream flow requirements for selected fishes in the wild and scenic portion of the Missouri River. Montana Fish, Wildlife and Parks, Great Falls.

Gardner, W. M., and P. A. Stewart. 1987. The fishery of the lower Missouri River, Montana. Montana Department of Fish, Wildlife and Parks, Report FW-2-R, Helena.

Graham, P. J., R. F. Penkal, and L. Peterman. 1979. Aquatic studies of the Yellowstone River. Montana Fish and Game, Report REC-ERC-79-8, Helena.

Haddix, M. H., and C. C. Estes. 1976. Lower Yellowstone River fishery study. Montana Fish and Game, Helena.

Hampton, J. 1997. Estimates of tag-reporting and tag-shedding rates in a large-scale tuna tagging experiment in the western tropical Pacific Ocean. Fishery Bulletin 95:68–79.

Hart, L. G., and R. C. Summerfelt. 1975. Surgical procedures for implanting ultrasonic transmitters into flathead catfish (*Pylodictis olivaris*). Transactions of the American Fisheries Society 104:56–59.

Helfrich, L. A., C. Liston, S. Hiebert, M. Albers, and K. Frazer. 1999. Influence of low-head diversion dams on fish passage, community composition, and abundance in the Yellowstone River, Montana. Rivers 7:21–32.

Hesse, L. W. 1994. The status of Nebraska fishes in the Missouri River, 6. Sauger (Percidae: *Stizostedion canadense*). Transactions of the Nebraska Academy of Sciences 21:109–121.

Hiebert, S. D., R. Wydoski, and T. J. Parks. 2000. Fish entrainment at the lower Yellowstone diversion dam, Intake Canal, Montana, 1996–1998. U.S. Bureau of Reclamation, Denver.

Jaeger, M. E. 2005. Southeast Montana warmwater streams investigations. Montana Department of Fish, Wildlife and Parks, Report F-78-R-5, Helena.

Lawal, H. B., and G. J. G. Upton. 1984. On the use of X^2 as a test of independence in contingency tables with small cell expectations. Australian Journal of Statistics 26:75–85.

Leopold, L. B., M. G. Wolman, and J. P. Miller. 1992. Fluvial processes in geomorphology. Dover Publications, Mineola, New York.

Maceina, M. J., P. W. Bettoli, S. D. Finely, and V. J. DiCenzo. 1998. Analyses of the sauger fishery with simulated effects of a minimum size limit in the Tennessee River of Alabama. North American Journal of Fisheries Management 18:66–75.

MacRitchie, I. C., and E. R. Armstrong. 1984. An incentive program to increase angler tag returns. North American Journal of Fisheries Management 4:129–130.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals. Kluwer Academic Press, Dordrecht, The Netherlands.

Marcy, B. C., and R. C. Galvin. 1973. Winter–spring sport fishery in the heated discharge of a nuclear power plant. Journal of Fish Biology 5:541–547.

McMahon, T. E. 1999. Status of sauger in Montana. Montana Fish, Wildlife and Parks, Helena.

McMahon, T. E., and W. M. Gardner. 2001. Status of sauger in Montana. Intermountain Journal of Science 7:1–21.

Montana Bureau of Mines and Geology. 1979. Geologic map of the Hysham 30′ × 60′ quadrangle, Montana, 1:100,000. Montana Bureau of Mines and Geology, Open File Report 371, Butte.

Montana Bureau of Mines and Geology. 1980. Geologic map of the Terry 30′ × 60′ quadrangle, Montana, 1:100,000. Montana Bureau of Mines and Geology, Open File Report 284, Butte.

Montana Bureau of Mines and Geology. 1981a. Geologic map of the Sidney 30′ × 60′ quadrangle, Montana, 1:100,000. Montana Bureau of Mines and Geology, Open File Report 277, Butte.

Montana Bureau of Mines and Geology. 1981b. Geologic map of the Wibaux 30′ × 60′ quadrangle, Montana, 1:100,000. Montana Bureau of Mines and Geology, Open File Report 282, Butte.

Montana Bureau of Mines and Geology. 1998. Geologic map of the Glendive 30′ × 60′ quadrangle, Montana, 1:100,000. Montana Bureau of Mines and Geology, Open File Report 371, Butte.

Montana Bureau of Mines and Geology. 2000. Geologic map of the Billings 30′ × 60′ quadrangle, Montana, 1:100,000. Montana Bureau of Mines and Geology, Geologic Map Series 59, Butte.

Montana Bureau of Mines and Geology. 2001a. Geologic map of the Miles City 30′ × 60′ quadrangle, Montana, 1:100,000. Montana Bureau of Mines and Geology, Open File Report 426, Butte.

Montana Bureau of Mines and Geology. 2001b. Geologic map of the Forsyth 30′ × 60′ quadrangle, Montana, 1:100,000. Montana Bureau of Mines and Geology, Open File Report 425, Butte.

Natural Resources Conservation Service. 2002. Lower Yellowstone River corridor color infrared digital orthophotography, Montana. Natural Resources and Conservation Service, Bozeman. Available: www.nris.state.mt.us/yellowstone/LowerYel/LowerYelPhotos.html (April 2004).

Nelson, W. R. 1968. Reproduction and early life history of sauger, *Stizostedion canadense*, in Lewis and Clark Lake. Transactions of the American Fisheries Society 97:159–166.

Nelson, W. R. 1969. Biological characteristics of the sauger population in Lewis and Clark Lake. U.S. Bureau of Sport Fisheries and Wildlife Technical Papers 21.

O'Driscoll, R. L. 1998. Description of spatial pattern in seabird distributions along line transects using neighbor *K* statistics. Marine Ecology Progress Series 165:81–94.

Olson, D. E., D. H. Schupp, and V. Macins. 1978. A hypothesis of homing behavior of walleyes as related to observed patterns of passive and active movement. Pages 52–57 *in* R. L. Kendall, editor. Selected coolwater fishes of North America. American Fisheries Society, Bethesda, Maryland.

Pegg, M. A., J. B. Layzer, and P. W. Bettoli. 1996. Angler exploitation of anchor-tagged saugers in the lower Tennessee River. North American Journal of Fisheries Management 16:218–222.

Pegg, M. A., P. W. Bettoli, and J. B. Layzer. 1997. Movement of saugers in the lower Tennessee River determined by radio telemetry, and implications for management. North American Journal of Fisheries Management 17:763–768.

Penkal, R. F. 1992. Assessment and requirements of sauger and walleye populations in the Lower Yellowstone River and its tributaries. Montana Department of Fish, Wildlife and Parks, Helena.

Rabeni, C. F., and R. B. Jacobson. 1993. Geomorphic and hydraulic influences on the abundance and distribution of stream centrarchids in Ozark, USA streams. Polskie Archiwum Hydrobiologii 40:87–99.

Rawson, M. R., and R. L. Scholl. 1978. Reestablishment of sauger in western Lake Erie. Pages 261–265 *in* R. L. Kendall, editor. Selected coolwater fishes of North America. American Fisheries Society, Special Publication 11, Bethesda, Maryland.

Rehwinkel, B. J. 1978. Powder River aquatic ecology project. Montana Fish and Game, Helena.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.

Roscoe, J. T., and J. A. Byars. 1971. An investigation of the restraints with respect to sample size commonly imposed on the use of the chi-square statistic. Journal of the American Statistical Association 66: 755–759.

Ross, M. J., and C. F. Kleiner. 1982. Shielded-needle technique for surgically implanting radio-frequency transmitters in fish. Progressive Fish-Culturist 44: 41–43.

Schlosser, I. J. 1991. Stream fish ecology: a landscape perspective. BioScience 41:704–712.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin 184.

Seber, G. A. F. 1982. The estimation of animal abundances and related parameters. Blackburn Press, Caldwell, New Jersey.

Silverman, A. J., and W. D. Tomlinsen. 1984. Biohydrology of mountain fluvial systems: the Yellowstone, part I. U.S. Geological Survey, Completion Report G-853–02, Reston, Virginia.

Smith, D. R., K. P. Burnham, D. M. Kahn, X. He, C. J. Goshorn, K. A. Hattala, and A. W. Kahnle. 2000. Bias in survival estimates from tag-recovery models where catch-and-release is common, with an example from Atlantic striped bass (*Morone saxatilis*). Canadian Journal of Fisheries and Aquatic Sciences 57:886–897.

St. John, R. T. 1990. Sauger (*Stizostedion canadense*) abundance and spawning movements in the Fort Loudoun tailwaters, Tennessee. Master's thesis. Tennessee Tech University, Cookeville.

Swedberg, S. 1985. Mid-Yellowstone River study. Montana Fish, Wildlife and Parks, Report F-20-R-29, Helena.

Van Den Avyle, M. J., and R. S. Hayward. 1999. Dynamics of exploited fish populations. Pages 127–166 *in* C. C. Kohler and W. A. Hubert, editors. Inland fisheries management in North America. American Fisheries Society, Bethesda, Maryland.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–138.

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California.

White, R. G., and R. G. Bramblett. 1993. The Yellowstone River: its fish and fisheries. Pages 396–414 *in* L. W. Hesse, C. B. Stalnaker, N. G. Benson, and J. R. Zuboy, editors. Restoration planning for the rivers of the Mississippi River ecosystem. National Biological Survey, Biological Report 19, Washington, D.C.

Winter, J. D. 1996. Advances in underwater biotelemetry. Pages 555–590 *in* B. R. Murphy and D. W. Willis, editors. Fisheries techniques. American Fisheries Society, Bethesda, Maryland.

Zale, A. V., and M. B. Bain. 1994. Estimation of tag-reporting rates with postcards as tag surrogates. North American Journal of Fisheries Management 14:208–211.

Zar, J. H. 1999. Biostatistical analysis. Prentice-Hall, Upper Saddle River, New Jersey.