Transactions of the American Fisheries Society 130:1006–1025, 2001

Habitat Use and Movements of Pallid and Shovelnose Sturgeon in the Yellowstone and Missouri Rivers in Montana and North Dakota

ROBERT G. BRAMBLETT* AND ROBERT G. WHITE

U.S. Geological Survey, Montana Cooperative Fishery Research Unit,[1]
Department of Ecology, Montana State University−Bozeman, Bozeman, Montana 59717, USA

Abstract.—We observed the habitat use and movements of 24 pallid *Scaphirhynchus albus* and 27 shovelnose *S. platorynchus* sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota. Pallid sturgeon used sandy substrate more often than shovelnose sturgeon, as well as greater depths; both species used similar current velocities. Pallid sturgeon used river channels with greater widths, midchannel bars, frequent islands, and subclimax riparian vegetation more often than shovelnose sturgeon. Both species moved up to 15 km/d and moved during all seasons and diel periods, but they moved less during fall and winter; ranges of activity among the most wide-ranging individuals exceeded 250 river kilometers (rkm). Pallid sturgeon used the lower 28 rkm of the Yellowstone River in spring and summer, shifting to the Missouri River below the confluence of the Yellowstone River in fall and winter. Shovelnose sturgeon were most often observed in the Yellowstone River in all seasons. Aggregations in late spring and early summer suggest that pallid sturgeon may spawn in the lower 14 rkm of the Yellowstone River. The infrequent use by both species of the Missouri River from Fort Peck Dam downstream to the Yellowstone River confluence may be due to altered ecological conditions associated with the dam and emphasizes the importance of natural river processes for these species.

Pallid sturgeon *Scaphirhynchus albus* were listed as endangered in 1990 (Dryer and Sandvol 1993), and shovelnose sturgeon *S. platorynchus* abundance has also declined (Keenlyne 1997). Basic information on habitat requirements and movements of pallid sturgeon, which are needed to assist recovery efforts, are lacking (Dryer and Sandvol 1993). More information exists for shovelnose sturgeon, but no previous study has compared habitat use and movements of these two species in sympatry. The original distributions of these two species suggest that they have different habitat requirements. Pallid sturgeon were found in the lower Mississippi, Missouri and Yellowstone rivers, and occasionally in tributaries (Forbes and Richardson 1905; Cross 1967; Brown 1971; Lee et al. 1980; Keenlyne 1989). Shovelnose sturgeon, which are sympatric with pallid sturgeon over their entire range, also occur in most of the larger tributaries (Bailey and Cross 1954; Lee et al. 1980; Keenlyne 1997).

Most authors attribute the decline of pallid and shovelnose sturgeon to the massive habitat alterations that have taken place throughout their range (Kallemeyn 1983; Gilbraith et al. 1988; Keenlyne 1989; Dryer and Sandvol 1993; Keenlyne 1997). Since 1937, six mainstem dams have been built on the Missouri River. About 51% of the pallid sturgeon's range has been channelized for barge navigation, 28% has been impounded, and the remaining 21% is below dams, where temperature, flow, and sediment dynamics are altered (Keenlyne 1989). Most studies describing habitat use and movements for pallid and shovelnose sturgeon have been conducted in altered habitats (Helms 1974; Carlson et al. 1985; Hurley et al. 1987; Erickson 1992; Curtis et al. 1997; Quist et al. 1999). Our study area is part of a recovery-priority area for pallid sturgeon, based on recent records of pallid sturgeon occurrence and a high likelihood that this area provides suitable habitat (Dryer and Sandvol 1993). Moreover, the lower Yellowstone River, is the longest unregulated river in the contiguous United States (White and Bramblett 1993), and the Missouri River below the Yellowstone River confluence retains much of its natural character due to the influence of the Yellowstone River. Thus, the objective of this study was to describe and compare habitat use and movements of pallid and shovelnose sturgeon in this area, one of the least-disturbed habitats remaining within the range of these two species.

* Corresponding author: bbram@montana.edu
[1] The unit is jointly supported by Montana State University–Bozeman, the Montana Department of Fish, Wildlife, and Parks, and the U.S. Geological Survey, Biological Resources Division.

Received February 27, 2001; accepted June 12, 2001

Study Area

The study area included the lower 113 river kilometers (rkm) of the Yellowstone River from Intake Diversion Dam at Intake, Montana, to its confluence with the Missouri River (hereafter referred to as the confluence) in North Dakota, and about 375 rkm of the Missouri River from Fort Peck Dam in Montana downstream to the headwaters of Lake Sakakawea in North Dakota. The study area had three distinct river reaches:

(1) The Yellowstone River (rkm 0.0–113.0). This reach extends from the confluence of the Missouri River upstream to Intake Diversion Dam. Discharge, temperature, turbidity, sediment load, and suspended sediment are higher in the Yellowstone River than in the Missouri River above their confluence (Shields et al. 1994) . The upper part of this reach (rkm 47–113) has numerous islands, bars, backwaters, and chutes; a primarily cobble and gravel substrate; a sinuous to irregular channel pattern (Kellerhals et al. 1976); and an average slope in a representative reach of 0.046% (Koch et al. 1977). Near Sidney, Montana, about 47 km above the confluence with the Missouri River, the slope declines and sand becomes the predominant substrate, but islands, bars, and lateral channel habitats remain common.

(2) The Missouri River above the confluence (hereafter shortened to ATC; rkm 2,545.4–2,850.5). This reach extends from the confluence of the Yellowstone River upstream to Fort Peck Dam and includes the ''dredge cuts'' (i.e., areas deepened by dredging during dam construction). In contrast to the Yellowstone River, the hydrograph, sediment dynamics, and temperature regime of this reach of the Missouri River have been altered since the completion of Fort Peck Dam in 1937 (Hesse 1987; Latka et al. 1993). Substrate in the upper part of the reach is cobble and gravel due to channel degradation; substrate in the channel below the dam becomes predominantly sandy in the lower 250 rkm of the reach (Gardner and Stewart 1987). Gradient is generally lower than in the Yellowstone River, ranging from 0.011% to 0.028% (Tews 1994).

(3) The Missouri River below the confluence (hereafter shortened to BTC; rkm 2,545.4–2,475.0). This reach extends from the headwaters of Lake Sakakawea, near Williston, North Dakota upstream to the confluence of the Yellowstone River, located about 5 km east of the Montana–North Dakota border. The Missouri River recovers much of its natural character in this reach because of the influence of the Yellowstone River. Sandbars and islands are common, and depths are greater than in the Yellowstone River or the Missouri River ATC.

Methods

Adult pallid and shovelnose sturgeon were captured by drifting mono- or multifilament trammel or gill nets (1.8 m deep × 15–37 m long; Krentz 1994; Tews 1994). One pallid sturgeon was captured by hand by scuba divers just downstream of Fort Peck Dam and five shovelnose sturgeon were obtained from anglers at Intake Diversion Dam. Captured sturgeon were weighed, measured, and fitted with transmitters. Pallid and shovelnose sturgeon were distinguished in field by location and size of their barbels, body size, and color (Bailey and Cross 1954; Pflieger 1975; Keenlyne et al. 1994). We consider that the pallid and shovelnose sturgeon used in this study were representative of the populations in the study area because they were captured in areas where they were known to occur most commonly, according to the biologists from Montana Fish, Wildlife, and Parks and the U.S. Fish and Wildlife Service who captured most of the sturgeons and had extensive experience in our study area.

Sturgeon movements and habitat use were monitored using radio and sonic transmitters. Transmitters were surgically implanted (Ross 1981), or attached to the base of the dorsal fin (Apperson and Anders 1990). After surgery, sturgeons were confined in quiet water for approximately 20 min before release.

Telemetry

Each radio and sonic transmitter had a unique frequency or pulsed code. An Advanced Telemetry Systems scanning radio receiver and a Sonotronics model USR-91 sonic receiver with a submersible directional hydrophone were used to locate fish. Telemetered fish were located using a combination of boat and aircraft searches. From May through August 1992, May through November 1993, and May through September 1994 fish were located during approximately biweekly surveys, first by aircraft search and then, more precisely, by boat. During the other periods, fishes were located approximately monthly via aircraft. To avoid bias and provide good temporal and spatial coverage of samples, we followed a random sampling scheme for collecting habitat-use data. The study area was divided into six sampling units, each approximately 32 rkm in length. Following aerial relocations, the units containing telemetered fish were listed and the sequence of sampling units to be surveyed was randomly drawn without replacement.

Radio signals from telemetered sturgeons were first detected with a boat-mounted whip antenna at a range of 400 m or more. Specific locations were then determined by triangulating the radio signal from shore with a directional loop antenna. Blind tests with transmitters placed in the river showed this technique was accurate to within approximately 3 m. We monitored the fish for 10 min and classified it as moving or stationary. We recorded the time of the relocation and assigned it to a diel category: day ($\geq$1 h after sunrise until $\geq$ 1 h before sunset), dusk ($<$1 h before sunset until $<$1 h after sunset), dark ($\geq$1 h after sunset until $\geq$1 h before sunrise), or dawn ($<$1 h before sunrise until $<$1 h after sunrise). Latitude and longitude of relocations were determined with a global positioning system (GPS). Habitat was characterized at the site, as described below. Discharge data for the Yellowstone and Missouri rivers were obtained from U. S. Geological Survey gauging stations located at Sidney and Culbertson, Montana, respectively.

Habitat Characteristics

Substrate use and availability.—Because turbidity and water depth usually prevented visual determination, the predominant substrate for a fish's location was determined by tactile sensation as transmitted with a steel conduit (Hamilton and Bergersen 1984). Substrate was classed as fines and sand (0–4 mm in diameter), gravel and cobble (5–300 mm), or boulder and bedrock ($>$300 mm). Blind tests with known substrate validated this method.

Relative availability of substrate classes in the Yellowstone and lower Missouri rivers was estimated by randomly choosing *X* and *Y* coordinates on the plan view of the river channel as we proceeded downstream during daily sampling. The *X* coordinate was determined by choosing a random number between 1 and 9 that corresponded to a position in the channel cross section (0 was left bank, 10 was right bank). The Y coordinate was determined by choosing a random number between 1 and 10 that corresponded to minute of travel time downstream. Substrate was then classified at these randomly selected locations.

Depth, channel width, and current velocity.—A cross section of the channel at the fish's location was produced by following a transect perpendicular to the direction of the current while recording the bottom profile with a recording depth finder. The fish's location and the maximum depth in the channel cross section were recorded on the chart, and relative depth was calculated by dividing the depth at the fish's location by the maximum depth. Channel width was estimated with an optical rangefinder. We measured water velocities at 0.3 m above the bottom with a Marsh-McBirney model 201 portable current meter equipped with cable suspension system, or a General Oceanics model 2030R current velocity meter. Velocities were measured in triplicate, and a mean was calculated.

Macrohabitat.—The macrohabitat character for sturgeon locations was described by visually classifying features at two scales. First, channel pattern of the reach within approximately 0.5 km upstream and downstream of the fish's location was classified according to categories described by Kellerhals et al. (1976). Channel patterns were straight (very little curvature within the reach), sinuous (slight curvature having a total lateral extent of meandering of less than approximately two channel widths), irregular (occasional curves with a lateral meander width of less than approximately two channel widths), or irregular meanders (increased curves with a vaguely repeated pattern present). Second, the river's geomorphic condition within two channel widths of the fish's position was characterized as a straight reach or a curve (i.e., a reach within two channel widths of the curve's maximum bend). Islands and alluvial bars within two channel widths of the fish's location were recorded. Alluvial bars were defined as features with elevations lower than the valley floor without vegetation or having vegetation characteristic of an earlier sere than islands. In contrast, islands were relatively stable and vegetated and at or near the same elevation as the valley floor (Kellerhals et al. 1976). Alluvial bars were classified as: channel side bars; channel junction bars; point bars; and midchannel bars (Kellerhals et al. 1976). The sere of the island or bar was classified as: bare or pioneer (grass, forbs, seedling willows, or cottonwoods); willow–cottonwood thicket; young cottonwood forest; or mature cottonwood gallery forest or later sere.

Island density use and availability.—Island density was used as a measure of habitat complexity because islands create more than one flow channel and a diversity of depths and current velocities. Aerial photos taken in 1994 and USGS 7.5-min topographic maps were used to characterize the study area in terms of island density (Kellerhals et al. 1976) categories. The Missouri River ATC was not characterized because we rarely relocated sturgeons in this reach. Reaches were classified as: none (reaches ≥0.5 rkm from an island), single (a single island, no overlapping of islands), frequent (occasional overlapping of islands and average spacing between islands <10 river widths), or split channel (islands overlap other islands frequently or continuously and the number of flow channels was usually two or three).

Data Analysis

We tested the general hypotheses that there was no difference in use of substrate, depth, current velocity, and island density categories, or ranges of activity and movement rates between pallid and shovelnose sturgeon. Sample sizes in telemetry studies can be inflated when data are collected by continuously monitoring individuals (White and Garrott 1992), which brings into question the independence of such data. We considered habitat data collected on different days to be independent, whereas data collected during diel sampling were not considered independent. Therefore, we used all habitat data collected on different days, combined with one randomly selected observation per diel sampling period per fish as sample size for analysis of habitat variables.

We tested the normality of substrate, depth, channel width, current velocity, and movement rate data using the Komolgorov–Smirnov *D*-test (Neter et al. 1993). If the data were normal, *t*-tests or analysis of variance (ANOVA) were used to compare means for pallid and shovelnose sturgeon, whereas if the data were not normal, a Mann–Whitney *U*-test or Kruskal–Wallis *H*-test (Zar 1999) was used to compare sample distributions of data for pallid sturgeon versus shovelnose sturgeon.

Substrate.—Observations of substrate use for each individual fish were converted to proportions so that analyses were equally weighted among individuals with differing numbers of observations. Two aspects of substrate use were examined. First, we tested the hypothesis that substrate use by pallid and shovelnose sturgeon was the same with the Mann–Whitney *U*-test. Second, we tested whether use of substrate for each species was the same as availability by using the Wilcoxon paired-sample test (Zar 1999). The Wilcoxon paired-sample test allowed us to compare substrate use for each individual fish to the estimated proportions of substrate available in that individual's range of activity, rather than comparing substrate use for each individual fish to the entire range of the species within our study area.

Depth and current velocities.—We used ANOVA to test the following a priori hypotheses: (1) depth and current velocities used by pallid sturgeon and shovelnose sturgeon were not different, (2) depths and current velocities used by pallid and shovelnose sturgeon in the Yellowstone River were not different from those used in the Missouri River BTC, (3) difference in depth and current velocities between shovelnose and pallid sturgeon was the same in the Yellowstone River and the Missouri River BTC (i.e., no interaction between species and rivers), and (4) variance among means of depth and current velocity used by species and individual fish in each river was equal to zero. Data for the Missouri River ATC were not included in the ANOVA models because of small sample size. We did not compare use versus availability of depths and current velocities because the availability of these habitat features varies with discharge.

Island density use and availability.—To test the hypothesis that island density categories for pallid and shovelnose sturgeon as species and as individuals were used in proportion to availability, we used chi-square analysis followed by calculation of a Bonferroni *Z*-test to determine if specific categories were used more or less than expected at the recommended α of 0.10 (Nue et al. 1974 ; Alldredge and Ratti 1992). Availability of island-density categories was calculated according to the hypothesis being tested. For example, when testing for selection of all pallid sturgeon pooled together, relative availability of island densities for the entire pallid sturgeon range within the Yellowstone and Missouri (BTC) rivers was used. When testing for selection by an individual fish, only the reaches in that individual's range of activity (distance between the farthest upstream and downstream locations of a given fish) were used. Individual variation in selecting island-density categories was examined by testing selection of pallid sturgeon with more than 10 observations and shovelnose sturgeon with more than 8 observations.

Results

We equipped 24 adult pallid sturgeon and 27 adult shovelnose sturgeon with transmitters. Pallid sturgeon fork length varied from 1,151 to 1,600 mm, and weight varied from 10.7 to 28.2 kg; shovelnose sturgeon fork length varied from 581 to 947 mm, and weight varied from 0.8 to 4.2 kg. We observed habitat use and movements of these in-

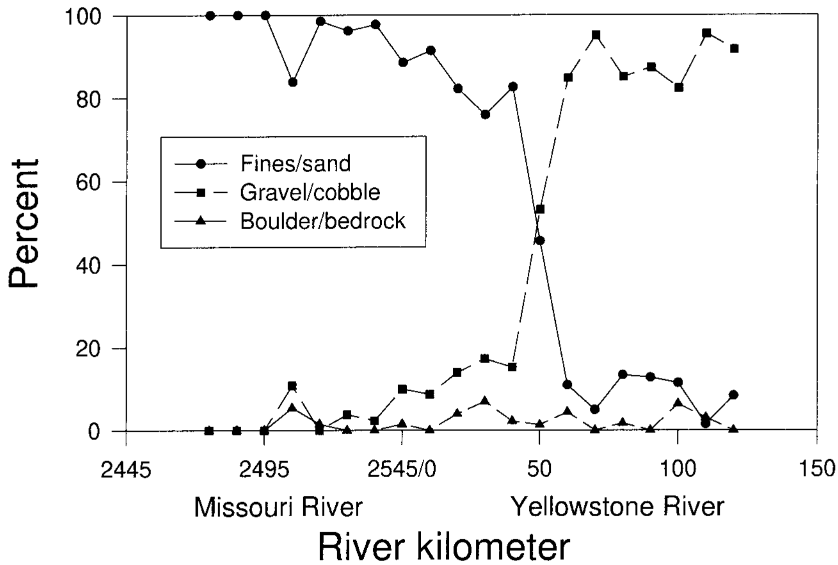

FIGURE 1.—Distribution of substrate types in the Yellowstone River and the Missouri River downstream of the confluence with the Yellowstone River, 1993–1994, as estimated from 1,273 randomly chosen points. River kilometer 2,545/0 is the confluence of the Missouri and Yellowstone rivers, river kilometers 0–150 are in the Yellowstone River, and river kilometers 2,445–2,545 are in the Missouri River.

dividual fishes for varying lengths of time, because of varying transmitter life, during the period August 1991 through November 1994.

Substrate

We estimated the distribution of substrate from measurements at 1,273 randomly selected points. Substrate in the Missouri River BTC and in the lower 50 rkm of the Yellowstone River was predominantly sand, whereas substrate in the upper reaches of the Yellowstone River in our study area was predominantly gravel and cobble. Boulder and bedrock substrate was rare in the study area (Figure 1).

Pallid sturgeon ($N = 22$ fish) used fines and sand significantly more than shovelnose sturgeon (Mann–Whitney U, $P = 0.00006$). Shovelnose sturgeon ($N = 21$ fish) used gravel and cobble significantly more than pallid sturgeon ($P = 0.000005$; Figure 2). Use of boulder and bedrock substrate was not significantly different between the two species ($P = 0.90$).

Pallid sturgeon used gravel and cobble substrate at a rate (proportion) less than its availability (Wilcoxon paired-sample, $P = 0.003$), whereas their use of sand ($P = 0.46$) and boulder ($P = 0.25$) was in proportion to availability. Shovelnose sturgeon used sand (Wilcoxon paired-sample, $P = 0.21$) and gravel and cobble ($P = 0.19$) substrates in proportion to availability, but use of boulder substrate was less than availability ($P = 0.02$).

Depth

Pallid sturgeon used depths ranging from 0.6 to 14.5 m (mean ± SD = 3.3 ± 2.1, $N = 164$) compared with 0.9–10.1 m for shovelnose sturgeon (2.3 ± 1.2, $N = 147$). Depths used by pallid and shovelnose sturgeon varied significantly among individual fish (ANOVA, $P = 0.04$), but pallid sturgeon used greater depths more often than shovelnose sturgeon (ANOVA, $P = 0.02$; Figure 3).

Mean maximum depth in the channel cross-section at pallid sturgeon locations (4.4 m ± 1.3, $N = 137$) was greater (ANOVA, $P = 0.02$) than at shovelnose sturgeon locations (3.1 m ± 1.3, $N = 117$; Figure 3). Maximum channel cross-section depths were almost significantly greater in the Missouri River BTC than in the Yellowstone River (ANOVA, $P = 0.05$), and there was significant variance among individuals (ANOVA, $P = 0.004$). The mean relative depth (depth at fish location/maximum depth in channel cross section) for pallid sturgeon locations was 0.70 ($N = 134$, SD = 0.22), which was almost significantly (ANOVA, $P = 0.10$) less than the mean relative depth of 0.78 for shovelnose sturgeon ($N = 117$, SD = 0.18). Use of relative depths among individual pallid and

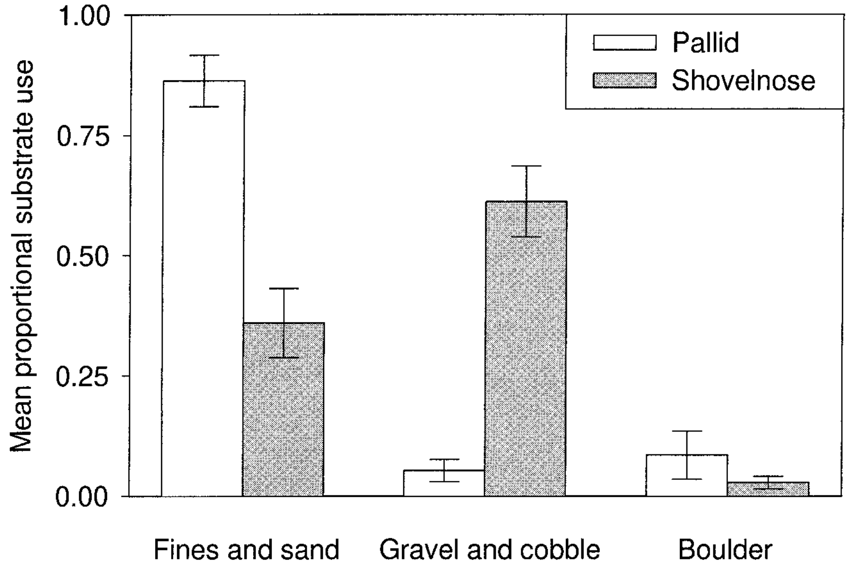

FIGURE 2.—Mean proportional use of substrate by pallid (*N* = 22) and shovelnose (*N* = 21) sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992–1994. Error bars are ±1 SE.

shovelnose sturgeon did not vary significantly (ANOVA, *P* = 0.18).

Current Velocity and Channel Width

Current velocities at pallid and shovelnose sturgeon locations overlapped (Figure 4), but the overall mean bottom velocity at pallid sturgeon locations of 0.65 m/s (*N* = 173, SD = 0.28) was significantly less than for shovelnose sturgeon (*t*-test, *P* = 0.0026), which was 0.78 m/s (*N* = 119, SD = 0.33). However, ANOVA revealed that this difference was attributable to location in the Missouri River BTC, where bottom velocities at fish locations were lower than at fish locations in the Yellowstone River (ANOVA, *P* = 0.0079). Bottom velocities used by the two species were not significantly different (ANOVA, *P* = 0.14), nor was variance in use of bottom velocities among individual pallid and shovelnose sturgeon (*P* = 0.78).

Channel widths at pallid sturgeon locations varied from 110 to 1,100 m (mean = 324 m, *N* = 144) and were significantly greater (Mann–Whitney *U*, *P* < 0.000001) than at shovelnose sturgeon locations, where width varied from 25 to 800 m (mean = 208 m; *N* = 161).

Macrohabitat

The channel pattern at pallid sturgeon locations (*N* = 212) was primarily sinuous or irregular; straight channels and irregular meanders were rarely used. Shovelnose sturgeon relocations (*N* = 147) were also observed most often in sinuous channels, but observations were more evenly distributed among channel types (Figure 5).

At the scale of within two channel widths, most pallid and shovelnose sturgeon locations were in straight reaches (93.8% and 92.6%, respectively), as opposed to areas near the apex of channel curves, which were rarely used. Both species were most often located near islands, and both species used reaches with alluvial bars less than reaches with islands (Figure 5). Reaches with neither bars nor islands were used least. Seral stage of islands and bars near pallid sturgeon locations was most often a sere preceding mature cottonwoods. Shovelnose sturgeon were found near islands with mature cottonwood forest more often than pallid sturgeon. When pallid sturgeon were located near an alluvial bar, it was most often a midchannel bar, whereas shovelnose sturgeon were most often found near channel side bars.

Island Density Use versus Availability

In our study area, reaches without islands, with a single island, with frequent islands, and with split channels composed 31.1, 7.7, 31.6, and 29.6%, respectively, of the Yellowstone River and the Missouri River BTC. Overall, pallid sturgeon association with island density categories was different than availability (χ^2, *P* < 0.00001, *N* = 246). Pallid sturgeon selected reaches with frequent islands and avoided reaches with no islands,

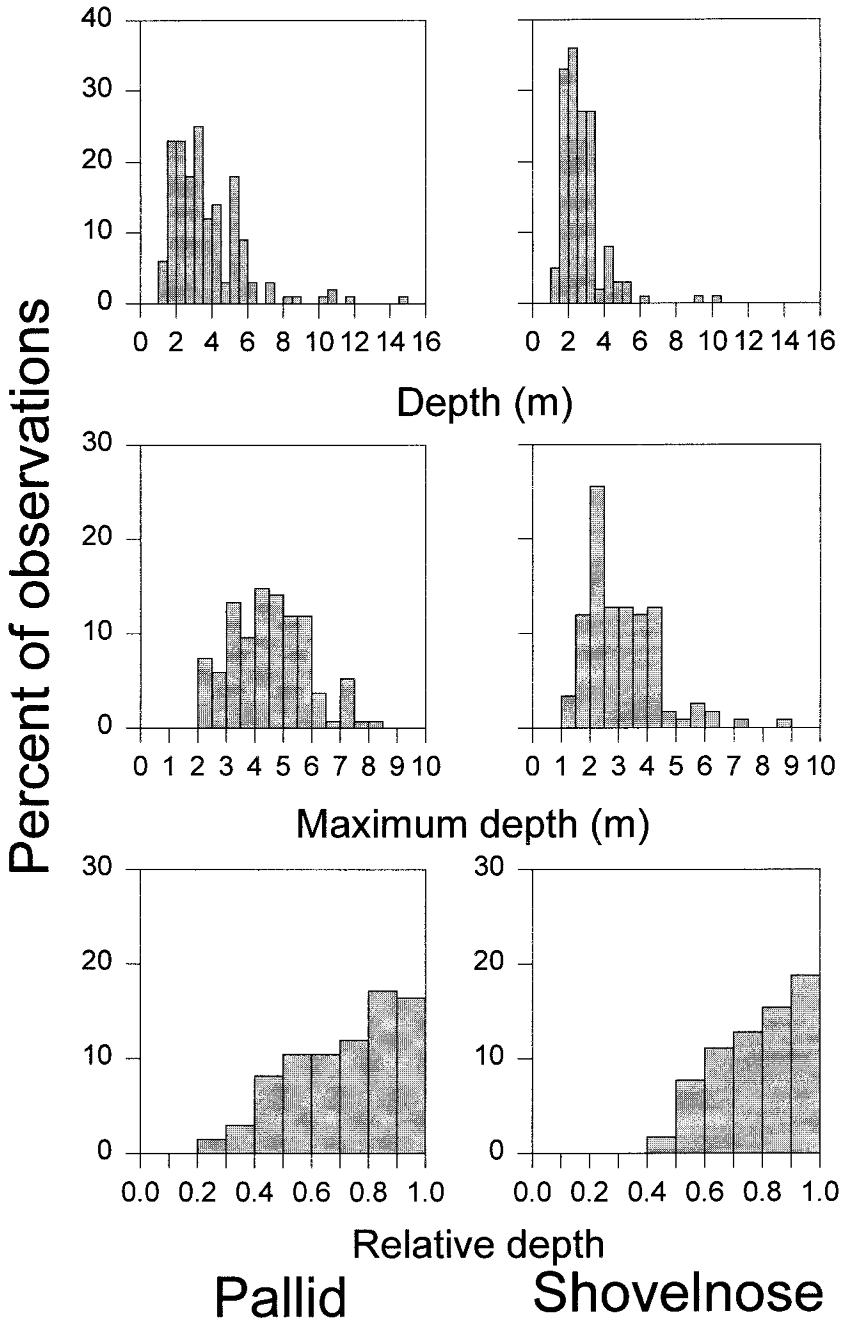

FIGURE 3.—Depth-based results for telemetered pallid and shovelnose sturgeon locations in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992–1994. Relative depth is the ratio of the depth at fish location to the maximum depth in the channel cross section.

single island reaches, and split channel reaches. Of 13 pallid sturgeon with more than 10 observations, 8 selected reaches with frequent islands, 6 avoided reaches with no islands, and 2 avoided split channel reaches (Bonferroni Z, $P < 0.10$). As a species, shovelnose sturgeon avoided single-island reaches (χ^2; $P < 0.04$, $N = 139$). However, only one of nine shovelnose sturgeon with eight

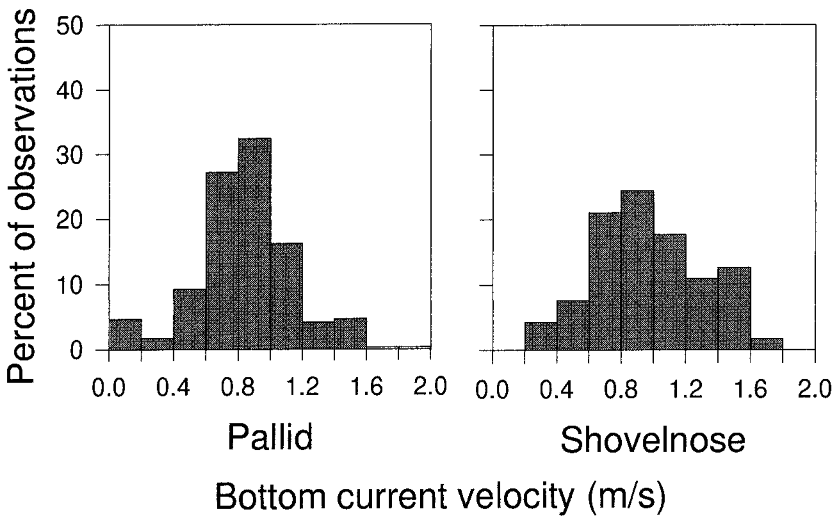

FIGURE 4.—Distributions of bottom current velocity at telemetered pallid and shovelnose sturgeon locations in the Yellowstone and Missouri rivers, Montana and North Dakota, 1992–1994.

or more observations had significant (Bonferroni Z, $P < 0.10$) island-density category sections (split channel).

Range of Activity

Range of activity was from 12.4 to 331.2 km for pallid sturgeon ($N = 24$, mean = 79.6 km, SD = 72.7) and was from 0 to 254.1 km for shovelnose sturgeon ($N = 24$, mean = 53.6 km, SD = 56.3). Days at large varied from 27 to 1,334 for pallid sturgeon and from 14 to 594 for shovelnose sturgeon. Range of activity was not significantly related to the number of relocations of pallid ($P = 0.20$) or shovelnose ($P = 0.43$) sturgeon. Seasonal ranges of activity were significantly different for both pallid (Kruskal–Wallis ANOVA, $P = 0.0004$) and shovelnose ($P = 0.0005$) sturgeon. Mean, median, and maximum ranges of activity were highest in spring or summer, and lowest in winter for both species (Figure 6).

Movement Rates

Pallid sturgeon were moving during 54% of relocations compared with 68% for shovelnose sturgeon relocations. Hourly movement rates ranged up to 9.5 km/h for pallid sturgeon and up to 6.6 km/h for shovelnose sturgeon. Upstream and downstream movement rates of either species were not significantly different (Mann–Whitney U, $P < 0.05$). Pallid sturgeon moved up to 21.4 km/d and shovelnose sturgeon up to 15.0 km/d (Figure 6). Pallid sturgeon hourly and daily movement rates were greater than for shovelnose sturgeon (Mann–Whitney U, $P < 0.05$). Seasonal daily movement rates for both species were significantly different (Kruskal–Wallis ANOVA, $P < 0.0001$). Mean, median, and maximum daily movement rates, from highest to lowest, were in spring (March 20–June 20), summer (June 21–September 22), fall (September 23–December 20), and winter (December 21–March 19) for both species.

Diel Movement

Both pallid and shovelnose sturgeon were observed moving during all four diel categories. Diel activity differed between pallid and shovelnose sturgeon. For example, during the day, the proportions of pallid and shovelnose sturgeon moving were 0.53 and 0.34, respectively, whereas at night the proportions were 0.37 and 0.52, respectively. Diel activity also differed between individual fish of both species. The three individual pallid sturgeon with the most observations ($N = 117$, 84, and 36) had daytime movement proportions of 0.68, 0.87, and 0.17. The three individual shovelnose sturgeon with the most observations ($N = 31$, 21, and 17) had daytime movement proportions of 0.23, 0.29 and 0.76.

Seasonal Distribution

The overall distribution of pallid sturgeon included the Yellowstone River and the Missouri River above and below the confluence (Figure 7). All observations of pallid sturgeon occurred in riverine portions of the study area, except for one that

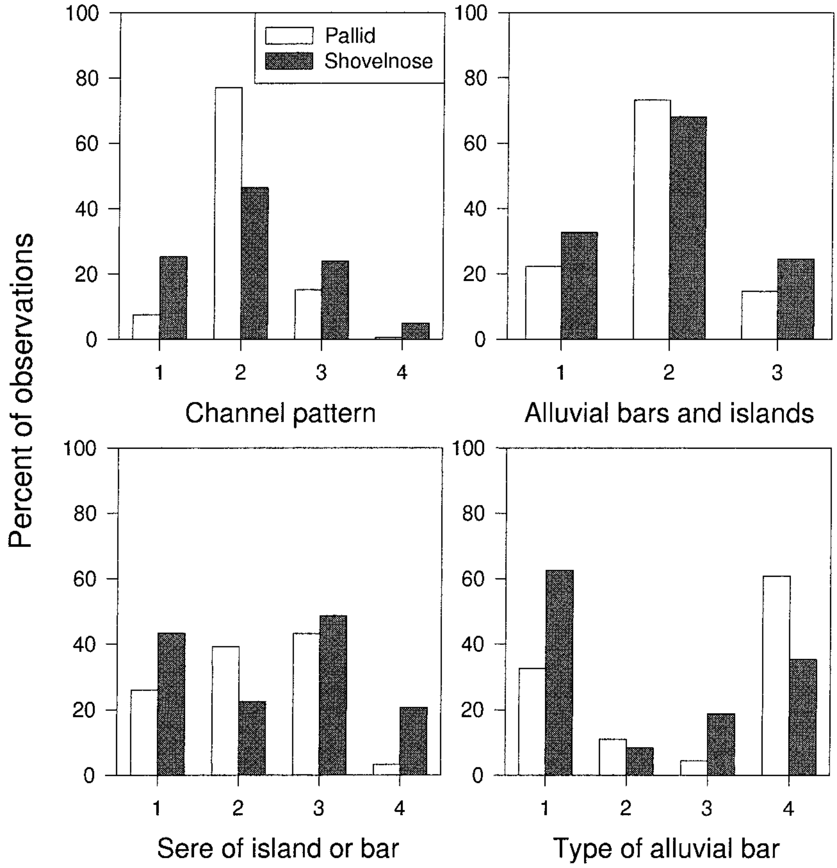

FIGURE 5.—Percent of location observations of telemetered pallid and shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992–1994, by channel pattern category (1 = straight, 2 = sinuous, 3 = irregular, 4 = irregular meanders), by alluvial bars and islands present or absent within reaches (1 = bar present, 2 = island present, 3 = neither present), by seral stage of island or bar (1 = bare or pioneer, 2 = willow/cottonwood thicket, 3 = young cottonwood forest, 4 = mature cottonwood gallery forest), and by alluvial bar category (1 = channel side bar, 2 = channel junction bar, 3 = point bar, 4 = midchannel bar).

was captured and subsequently relocated adjacent to the dredge cuts below Fort Peck Dam.

In spring, pallid sturgeon were distributed from rkm 2,476 in the Missouri River to rkm 114 in the Yellowstone River, just below Intake Diversion Dam. However, most locations (75%) were in the lower 28 km of the Yellowstone River or the 28 rkm of the Missouri River BTC (15%); 60% of observations were in the Yellowstone River from the confluence to rkm 12. The 2-km reach with the most locations was rkm 6–8 on the Yellowstone River, where 20% of observations occurred. The only pallid sturgeon that was relocated in the Missouri River ATC during spring was originally tagged below Fort Peck Dam.

The distribution of summer observations of pallid sturgeon was similar to spring, but more observations (39%) occurred in the Missouri River BTC. However 25% of the Missouri River observations were from a single individual. As in spring, the 2-km reach with the most locations was rkm 6–8 on the Yellowstone River, where 13% of observations occurred. Only four observations of pallid sturgeon were made in the Missouri River ATC. Except for the one pallid sturgeon that was tagged immediately below Fort Peck Dam, the uppermost location on the Missouri River was at rkm 2,764 (219 rkm ATC).

In fall, most (96%) pallid sturgeon observations were in the Missouri River BTC. Only three observations occurred in the Yellowstone River, where they were distributed to 6 rkm above the confluence. Except for the one pallid sturgeon captured just below Fort Peck Dam, only one obser-

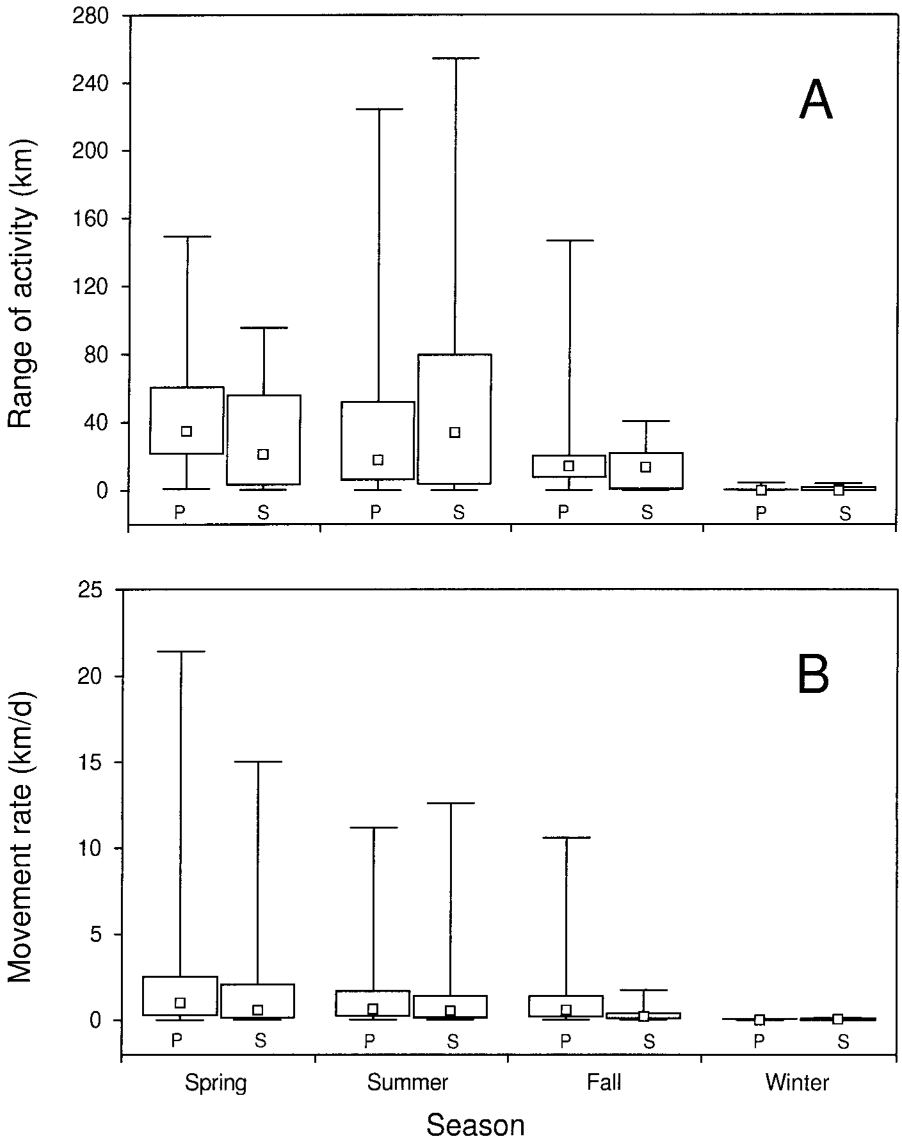

FIGURE 6.—**(A)** Seasonal range of activity (distance between the farthest upstream and downstream locations of a given fish) of telemetered pallid (P) sturgeon (summer N = 20, fall N = 16, winter N = 5, spring N = 22) and shovelnose (S) sturgeon (summer N = 22, fall N = 14, winter N = 7, spring N = 19) in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992–1994. **(B)** Movement rates by season measured at intervals greater than 24 h for telemetered pallid sturgeon (summer N = 132, fall N = 71, winter N = 14, spring N = 186) and shovelnose sturgeon (summer N = 157, fall N = 61, winter N = 10, spring N = 111) in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992–1994. Small boxes indicate median values, large boxes the 25th and 75th percentiles, and whiskers the minimum and maximum values.

vation was made in the Missouri River during fall, at rkm 2,676 (131 rkm ATC).

Winter distribution of pallid sturgeon was similar to fall. All winter relocations were between the confluence and 50 rkm below the confluence. The 2-km reach with the most observations (42%) was rkm 2,523–2,525 (about 20 rkm BTC).

Most shovelnose sturgeon were in Yellowstone River, but a few observations were in the Missouri River above and below the confluence (Figure 8).

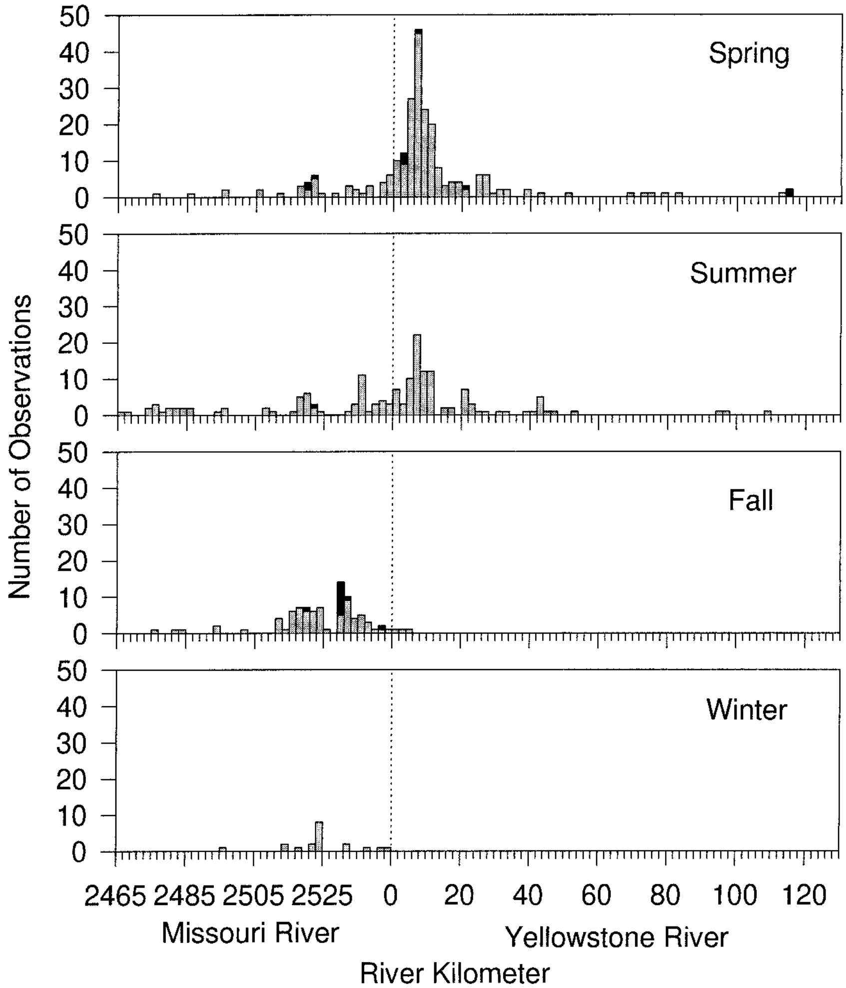

FIGURE 7.—Seasonal distributions of telemetered pallid sturgeon by river kilometer in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992–1994. River kilometers 2,465–2,545 are in the Missouri River below the confluence with the Yellowstone River, and river kilometers 0–130 are in the Yellowstone River. Black bars are capture locations, gray bars telemetry relocation sites.

All observations of telemetered shovelnose sturgeon occurred in riverine portions of the study area, except for two that were captured and subsequently located adjacent to the dredge cuts below Fort Peck Dam.

In spring, shovelnose sturgeon were distributed from rkm 2,531 in the Missouri River to rkm 114 in the Yellowstone River. Overall, 99% of observations were in the Yellowstone River. Most locations were in two general areas, rkm 0–28 (27%) and rkm 106–114 (51%). The 2-km reach with the most locations (17%) was on the Yellowstone River just below Intake Diversion Dam (rkm 114–116). Only one observation was from the upper Missouri River at rkm 2,562 (17 km ATC).

As with pallid sturgeon, the distribution of shovelnose sturgeon in summer was similar to that in spring. Shovelnose sturgeon were distributed from rkm 2,748 in the Missouri River to rkm 122 in the Yellowstone River. Most (94%) observations were in the Yellowstone River. The 2-km reach with the most locations (9%) was rkm 110–112 on the Yellowstone River. Just one observation during summer was in the Missouri River at rkm 2,748 (203 km ATC).

In contrast to pallid sturgeon, the distribution of shovelnose sturgeon in fall and winter was not markedly different from their distribution in spring and summer. During fall, telemetered shovelnose sturgeon were distributed from rkm 2,542 in the

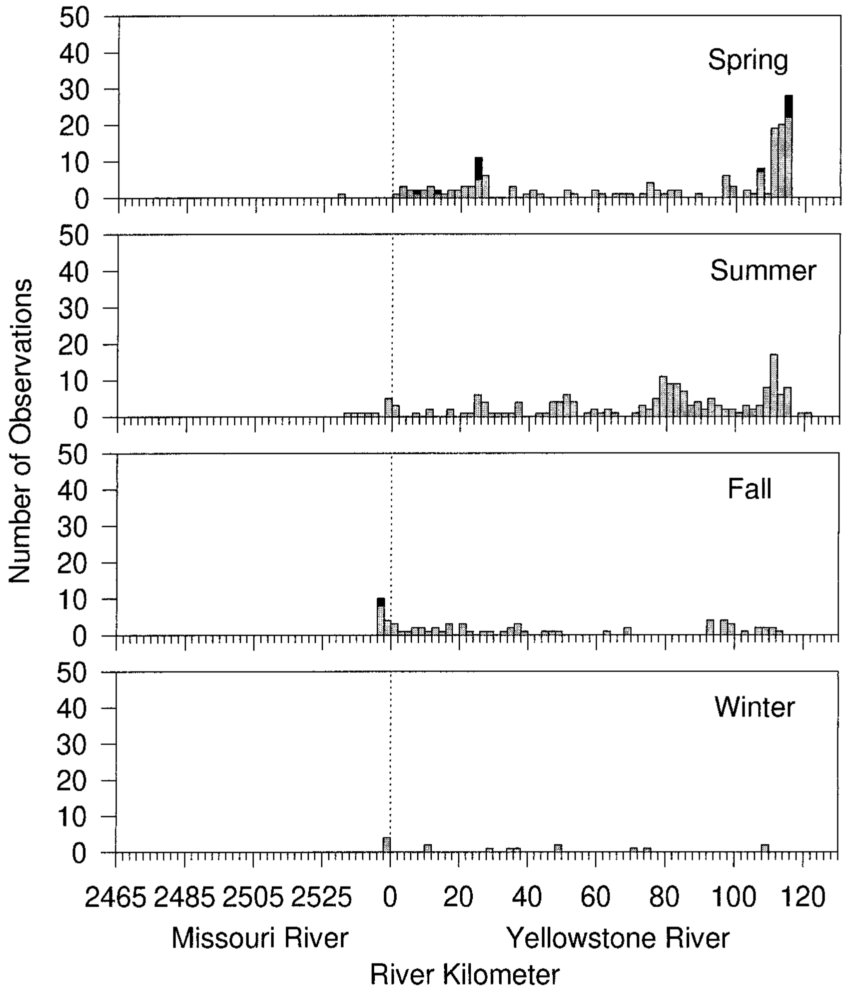

FIGURE 8.—Seasonal distributions of telemetered shovelnose sturgeon by river kilometer in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992–1994. River kilometers 2,465–2,545 are in the Missouri River below the confluence with the Yellowstone River, and river kilometers 0–130 are in the Yellowstone River. Black bars are capture locations, gray bars telemetry relocation sites.

Missouri River to rkm 113 in the Yellowstone River. The 2-km reach with the most locations (14%) was rkm 2,541–2,543 on the lower Missouri River, about 4 rkm BTC. Excluding one shovelnose sturgeon that was tagged below Fort Peck Dam, just one observation during fall was from the Missouri River at rkm 2,747 (202 km ATC).

In winter, shovelnose sturgeon were distributed from rkm 2,545 on the Missouri River to rkm 108 on the Yellowstone River. The 2-km reach with the largest number of locations (14%) was rkm 2,541–2,543 on the Missouri River, about 4 rkm BTC. Just one winter observation was from the Missouri River at rkm 2,747 (202 km ATC).

Movement Patterns

The movements of a pallid sturgeon captured in the lower Missouri River in April 1992 illustrates the general movement pattern we observed for this species (Figure 9). This individual displayed four characteristics typical of pallid sturgeon tagged near the confluence (Tews 1994): (1) movement upstream from the Missouri River BTC into the Yellowstone River in April, May, or June (100% of pallid sturgeon captured near the confluence displayed this characteristic, $N = 15$); (2) a period of residency in the Yellowstone River during May, June, or July (100%, $N = 19$); (3) movement downstream from the Yellowstone River to the Missouri

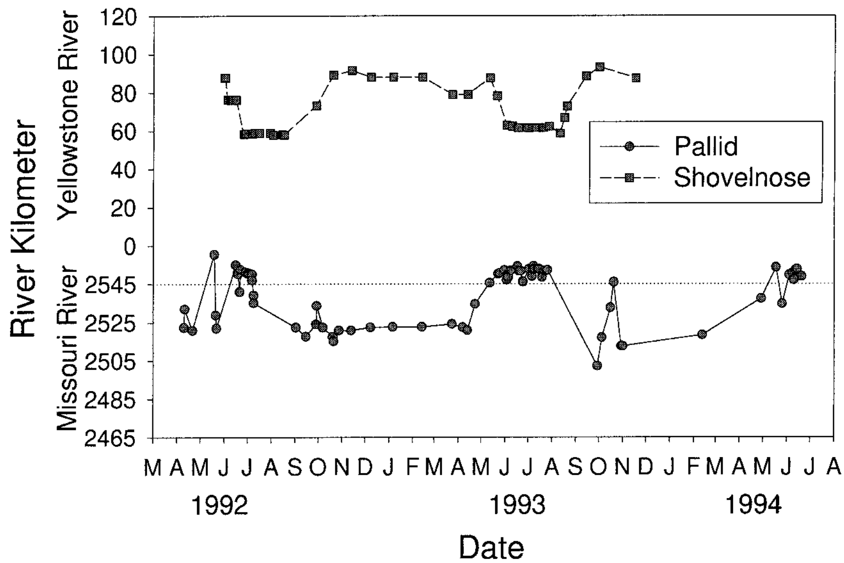

FIGURE 9.—Relocations, by river kilometer and month, of a pallid sturgeon and a shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota, 1992–1994.

River BTC during July, August, or September (71%, $N = 14$); and (4) a period of residency with limited movements in the Missouri River BTC during winter months (93%, $N = 14$).

In contrast to pallid sturgeon, most shovelnose sturgeon were found in the Yellowstone River in all seasons, and most were found farther upstream during winter. The movements of a shovelnose sturgeon captured in the Yellowstone River in June 1992 illustrate this pattern (Figure 9). Nine of 15 (60%) shovelnose sturgeon with a discernible movement pattern had fall or winter locations upstream of summer locations, whereas 6 (40%) had summer locations upstream of fall or winter locations. Two shovelnose sturgeon originally radiotagged below Intake Diversion Dam were later relocated upstream, having passed the diversion dam.

Movement into the Yellowstone and Missouri Rivers

On 31 occasions, pallid sturgeon ($N = 18$ individuals) located below the confluence were relocated upstream, having entered either the Yellowstone or Missouri (ATC) rivers. On 28 of these occasions the fish entered the Yellowstone River, and on 3 occasions the fish entered the Missouri River ATC. Thus, pallid sturgeon entered the Yellowstone River significantly more than expected by chance (chi-square test, $P = 0.000007$).

During periods when pallid sturgeon entered the Yellowstone River, discharge was significantly higher in the Yellowstone River (median = 251.3 m^3/s, SD = 283.2) than in the Missouri River ATC (median = 214.1 m^3/s, SD = 70.9; Mann–Whitney *U*, $P < 0.0000001$). During periods when pallid sturgeon entered the Missouri River ATC, discharge was significantly higher in the Missouri River ATC (median = 239.6 m^3/s, SD = 26.8) than in the Yellowstone River (median = 116.4 m^3/s, SD = 96.7, Mann–Whitney *U*, $P = 0.000005$).

Of 10 observations of six individual shovelnose sturgeon passing upstream of the confluence, 8 subsequent observations were in the Yellowstone River, which was almost significantly more than expected by chance (χ^2, $P = 0.06$). Median discharges in the Yellowstone River (median = 166.2 m^3/s, SD = 80.4) and Missouri River ATC (median = 214.1 m^3/s, SD = 61.9) were not significantly different (Mann–Whitney *U*, $P = 0.55$) during periods when shovelnose sturgeon entered the Yellowstone River. However, median discharge in the Missouri River ATC (median = 243.3 m^3/s, SD = 47.4) was significantly higher (Mann–Whitney *U*, $P = 0.008$) than in the Yellowstone River (median = 89.5 m^3/s, SD = 167.5) during the two periods when shovelnose sturgeon entered the Missouri River ATC.

Aggregations

We observed 29 aggregations (defined as three or more telemetered sturgeon in a 1-km reach on the same date) of pallid sturgeon and 20 aggregations of shovelnose sturgeon. Most (90%) pallid sturgeon aggregations were in the lower 13 rkm of the Yellowstone River in spring or summer; three fall and winter aggregations were observed in the Missouri River BTC. All shovelnose sturgeon aggregations were in the Yellowstone River, and most of these (65%) occurred from rkm 111.0 to rkm 114.2 during June and July. Two aggregations of shovelnose sturgeon were observed in fall in the Missouri River BTC.

Discussion

The majority of the range of pallid (Dryer and Sandvol 1993) and shovelnose (Keenlyne 1997) sturgeon has been affected by habitat alterations. Contemporary habitat use and movements of pallid and shovelnose sturgeon are probably different than before large-scale habitat alterations occurred. The unregulated Yellowstone River and the Missouri River below the Yellowstone River confluence to the headwaters of Lake Sakakawea represent the least-altered habitat available to pallid and shovelnose sturgeon and provide the best potential for determining habitat selection.

Sympatric shovelnose sturgeon have been proposed as a surrogate species to obtain inference about pallid sturgeon. Both species are often captured in the same gear sets (Carlson et al. 1985; Tews 1994), and hybrids have been reported (Phelps and Allendorf 1983; Carlson et al. 1985; Keenlyne et al. 1994), indicating periods of similar habitat use. Although we found that habitat use and movements of pallid sturgeon and shovelnose sturgeon were similar in certain aspects, important differences existed. Therefore, adult shovelnose sturgeon are of limited utility as surrogates for determining adult pallid sturgeon habitat needs.

Substrate

We observed different substrate-use behaviors for pallid and shovelnose sturgeon that are consistent with the distribution of the two species. Pallid sturgeon occur primarily in only the largest rivers (Cross 1967; Lee et al. 1980; Keenlyne 1989) where sand is the predominant substrate (Dryer and Sandvol 1993). Most pallid sturgeon captured in the Yellowstone and Missouri rivers in Montana and North Dakota are from predominantly sandy reaches (Krentz 1994; Tews 1994; Gardner 1995), although they are also occasionally captured in the gravel and cobble areas (Brown 1955, 1971; Watson and Stewart 1991; Gardner 1995). In the Missouri River in South Dakota, 89% of locations of telemetered pallid sturgeon larger than 5 kg were over sand or fines, whereas only 39% of those less than 5 kg were over sand or fines (Erickson 1992).

Shovelnose sturgeon are sympatric with pallid sturgeon in large rivers, but shovelnose sturgeon also occupy smaller rivers (Christenson 1975; Lee et al. 1980; Keenlyne 1997), where larger substrate is more likely to occur. In the Yellowstone and Missouri rivers in Montana, catch per unit effort of shovelnose sturgeon is generally higher in reaches predominated by gravel and cobble than in reaches of predominantly sand (Backes et al. 1994; Tews 1994). Shovelnose sturgeon in the Kansas River were often captured over gravel or rocky substrate (Quist and Guy 1999) but used sandy substrate in winter (Quist et al. 1999). In the Mississippi River, shovelnose sturgeon used sandy substrate most often (Hurley et al. 1987; Curtis et al. 1997) but also were associated with large rock substrate of wing dams (Hurley et al. 1987); gravel and cobble substrate was rare in this reach of the Mississippi River (Curtis 1990).

The differences in substrate use we observed may be related to food habits of the two species. Pallid sturgeon include fishes in their diet (Carlson et al. 1985), whereas shovelnose sturgeon are benthic invertivores (Barnickol and Starret 1951; Hoopes 1960; Held 1969; Helms 1974; Modde and Schmulbach 1977; Megargle 1997). We speculate that prey fishes may be easier for pallid sturgeon to capture over sand than over larger substrate. Because cobble and gravel substrate generally has higher benthic insect production than shifting, sandy substrate (Hynes 1970; Junk et al. 1989; Allan 1995), shovelnose sturgeon may find more food over cobble and gravel substrate. Perhaps smaller pallid sturgeon include more insects in their diet, which could explain the greater use of larger substrates by pallid sturgeon less than 5 kg (Erickson 1992).

Depth

Depths used by pallid and shovelnose sturgeon varied widely and overlapped substantially between the species. However, pallid sturgeon were found in deeper channels and at lesser relative depths than shovelnose sturgeon. Both species were found most often in the deepest half of the channel cross section. The differences in depths used between species and among individuals may be due to availability. Although we did not measure availability of depths, we observed that greater depths were more common in the downstream reaches of our study area where pallid sturgeon were found most often. Depths as great as 14.5 m for pallid sturgeon and 10.1 m for shovelnose sturgeon were used; however, there may have been a bias against relocations at great depths because of the attenuation of radio signals in deep, high-conductivity water (Winter 1996).

Mean depth at pallid sturgeon locations in our study area was about 1 m deeper than reported for the Missouri River above Fort Peck Reservoir in Montana (Gardner 1995) and about 1.4 m shallower than locations in the Missouri River in South Dakota (Erickson 1992). Similarly, mean depths of shovelnose sturgeon located in our study were shallower than those reported from telemetry studies in the Mississippi River (Hurley et al. 1987; Curtis et al. 1997) but deeper than in the Kansas River (Quist et al. 1999). Perhaps the pattern of using shallower depths in upstream areas and greater depths in downstream areas is due to the depth increases along the river continuum (Allan 1995) rather than to pallid and shovelnose sturgeon having different preferences in the different areas.

Current Velocity

The overall means of bottom current velocities used by pallid and shovelnose sturgeon were significantly different; however, this was because both species used higher current velocities in the Yellowstone River than in the Missouri River BTC. Because shovelnose sturgeon were most often found in the Yellowstone River, the overall mean velocity at their locations was higher. However, we do not know whether greater current velocities were available in the Yellowstone River and sturgeons used velocities in proportion to availability; nor do we know whether availability of velocities in the Yellowstone and Missouri rivers was the same but sturgeons used greater current velocities in the Yellowstone River.

In the Missouri River above Fort Peck Reservoir, mean bottom current velocities at pallid sturgeon locations were about 0.15 m/s faster than we found (Gardner 1994); in the Missouri River in South Dakota, velocities were 0.25 m/s slower for pallid sturgeon less than 5 kg and 0.47 m/s slower for those 5 kg or more (Erickson 1992). Mean current velocities at shovelnose sturgeon locations in our study were about 0.68 m/s faster than the mean observed for shovelnose sturgeon in Pool 13 of the Mississippi River (Curtis et al. 1997) and 0.85 m/s faster than in the Kansas River in winter (Quist et al. 1999). As with depth, these disparities in use of current velocities may reflect differences in availability rather than different preferences. Moreover, we did not statistically test for differences between the depths and velocities we observed and those from the cited studies, so there may not be a significant difference in means of these variables.

The wide, flat head, large pectoral fins, and flat ventral surface of shovelnose sturgeon allow them to maintain position in flowing water by substrate appression (Adams et al. 1997). This behavior, along with use of reduced velocity microhabitats next to the bottom may contribute to our observations of pallid and shovelnose sturgeon using relatively high-velocity areas.

Macrohabitat

Pallid sturgeon were more selective in their use of macrohabitat than shovelnose sturgeon. Pallid sturgeon were found most often in sinuous channels with subclimax seral-stage islands, midchannel bars, or both. Shovelnose sturgeon were also found most often in sinuous channels, but they used straight and irregular channels with channel side bars more frequently than pallid sturgeon, and sere of islands associated with shovelnose sturgeon locations more often included cottonwood gallery forests.

Pallid sturgeon selected reaches with frequent islands, located primarily in the lower 20 rkm of the Yellowstone River and avoided other categories of lesser or greater island density. Although similar reaches with frequent islands were found farther upstream in the Yellowstone River, pallid sturgeon may not have used them because sand substrate was less common there. Other factors, such as distribution of depths may limit pallid sturgeon use of reaches with the highest island densities. In contrast, shovelnose sturgeon were less selective with respect to use of reaches with different island-density categories.

Macrohabitats used by pallid sturgeon were diverse and dynamic, and their relatively restricted use suggests that features in these macrohabitats are more important to pallid sturgeon than to shovelnose sturgeon. Compared with relatively straight channels without islands or alluvial bars, reaches with sinuous channel patterns, abundant islands, and mid-channel bars have more diversity of depths, current velocities, and substrate, as well as more habitat features such as backwaters and side channels. Subclimax riparian vegetational seres are indicative of a dynamic river channel and riparian zone (Johnson 1993).

Perhaps pallid sturgeon selected more diverse and dynamic macrohabitats because these areas provided more abundant prey. Diverse macrohabitats that include features such as side channels and backwaters (Stalnaker et al. 1989) probably have more fish production than simpler habitats. Hesse and Sheets (1993) estimated that Missouri River fish production has declined as much as 216 million kg/year because of the decrease in habitat diversity and flood plain production caused by channelization and dam building. Funk and Robinson (1974) reported an 80% decline in commercial fish harvest from 1947 to 1963 on the Missouri River, and Hesse (1994) reported that abundance of seven cyprinid species in the Missouri River in Nebraska has been reduced by 70–98% from 1971 to 1993. Piscivorous fishes are thought to be more susceptible to habitat degradation and homogenization than fishes at lower trophic levels (Karr 1991). Thus, severed trophic links caused by habitat homogenization may partially explain why pallid sturgeon have declined more than shovelnose sturgeon.

Differences in macrohabitat use between pallid and shovelnose sturgeon may also be related to differences in spawning requirements of the two species. Suspected hybrids of pallid and shovelnose sturgeon have only rarely been captured in our study area (S. Krentz, U. S. Fish and Wildlife Service, personal communication), whereas they are more common in areas with reduced habitat diversity (Carlson et al. 1985; Dryer and Sandvol 1993; Keenlyne et al. 1994) where homogenized habitat may lead to a loss of reproductive isolation (Carlson et al. 1985).

Movements, Range of Activity, and Diel Activity

Pallid and shovelnose sturgeon exhibited rapid, long-range movements, and most of the longer movements occurred in spring and summer. These movements may have been associated with spawning activities because pallid and shovelnose sturgeon spawn in late spring to early summer (Forbes and Richardson 1905; Moos 1978; Keenlyne and Jenkins 1993; Keenlyne 1997). However, because female pallid (Keenlyne and Jenkins 1993) and shovelnose sturgeon (Moos 1978; Keenlyne 1997) probably do not spawn every year, some of these movements may be related to other factors, such as seasonal shifts between overwintering and summer feeding areas. For example, one pallid sturgeon that we monitored over 3 years had similar movement patterns each year.

Movement rates and ranges of activity for pallid and shovelnose sturgeon were significantly reduced during winter than during other seasons. Although this could have been an artifact of reduced sampling frequency in winter, it seems more likely that little movement occurred. Relatively sedentary winter behavior was also observed by Erickson (1992) for pallid sturgeon and Quist et al. (1999) for shovelnose sturgeon.

Telemetered pallid sturgeon in the Missouri River above Fort Peck Reservoir had similar movement patterns to those we observed, (i.e., the upstream-most locations and highest movement rates were in summer), but ranges of activity were less than we observed (Gardner 1994). Pallid sturgeon in the Missouri River in South Dakota also had smaller ranges of activity, which is probably related to reduced riverine habitat in the 137-km reach between dams in this area.

The highest proportion of observations on moving pallid sturgeon was during the day; the highest proportion of observations on moving shovelnose sturgeon was at night. However, because both pallid and shovelnose sturgeon also moved during other diel periods, they cannot be classified as strictly diurnal, nocturnal, or crepuscular. We also observed substantial individual variation in diel movement patterns.

In contrast to our findings, Erickson (1992) found that pallid sturgeon in the Missouri River in South Dakota moved more at night than during the day. The nocturnal activity may have been related to the reduced turbidity caused by Oahe Dam at the upstream end of Erickson's (1992) study area. Secchi disk depths in the Missouri River in South Dakota as high as 396 cm (average, 132 cm) exceeded readings at our pallid sturgeon locations (averaging 20 cm and rarely exceeding 100 cm; Bramblett 1996). Therefore, pallid sturgeon may become nocturnal in areas where natural turbidity has been reduced by dams.

We observed greater ranges of activity for shovelnose sturgeon than reported in some other studies. Researchers in the upper Mississippi River (Helms 1974; Hurley et al. 1987; Curtis et al. 1997) report ranges of activity that averaged up to 18.5 km for shovelnose sturgeon, compared with the overall mean of 53.1 km that we observed. However, the locks and dams in the upper Mississippi River may restrict movements of shovelnose sturgeon (Curtis et al. 1997). Modest movement was also reported for shovelnose sturgeon in the Red Cedar and Chippewa River system in Wisconsin (Christenson 1975), and in the Kansas River during winter (Quist et al. 1999). However, other studies have documented movements of shovelnose sturgeon in the Missouri River of up to 250 km (Moos 1978) and 534 km (Schmulbach 1974). Therefore, it is apparent that, when large reaches of unobstructed river are available, shovelnose sturgeon are capable of long-range movements. As in our study, the longest movements occurred during spring in the upper Mississippi River (Helms 1974; Hurley et al. 1987; Curtis 1990) and Missouri River (Moos 1978).

General Distribution

Pallid sturgeon were most often relocated in the Missouri River below the Yellowstone River confluence and the lower 28 km of the Yellowstone River; shovelnose sturgeon were found principally in the Yellowstone River. Pallid and shovelnose sturgeon appeared to avoid impounded areas; only one pallid sturgeon and no shovelnose sturgeon were observed within 10 km of the headwaters of Lake Sakakawea. Other researchers have reported avoidance of river impoundments by shovelnose sturgeon (Helms 1974; Curtis et al. 1997).

Most pallid sturgeon had a pronounced seasonal shift in locations from the Missouri River BTC in fall and winter, to the lower 28 km of the Yellowstone River in spring and summer. In contrast, the overall distribution of shovelnose sturgeon observations was not markedly different between seasons.

Aggregations in spring and early summer suggest locations of sturgeon spawning areas. A telemetered female pallid sturgeon with freely flowing eggs and a male pallid sturgeon with running milt were snagged by paddlefish anglers in 1993 (S. Krentz, U. S. Fish and Wildlife Service, personal communication). Locations of the telemetered female pallid sturgeon combined with aggregations of pallid sturgeon during late spring and early summer 1993 suggest that pallid sturgeon spawning areas may be in the lowermost 14 km of the Yellowstone River.

For shovelnose sturgeon, possible spawning locations are suggested by aggregations in the Yellowstone River at rkm 111.0–114.3 (directly below the Intake Diversion Dam) and at rkm 24.9–25.6. Shovelnose sturgeon may also concentrate below Intake Diversion Dam because it is a partial barrier to upstream movements (Stewart 1995).

Occasional aggregations of pallid and shovelnose sturgeon were observed in fall and winter but were more difficult to identify because fewer relocations were made in these seasons. However, other evidence indicates that pallid sturgeon aggregate during these periods. Tews (1994) captured 20 pallid sturgeon (7 in a single net) at one location in late September and October 1992 in the Missouri River BTC (rkm 2,531) during 4 d of netting (A. Tews, Montana Fish, Wildlife, and Parks, personal communication).

Pallid and shovelnose sturgeon were rarely located in the 305 rkm of riverine habitat on the Missouri River from Fort Peck Dam to the confluence of the Yellowstone River, and pallid sturgeon entered the free-flowing Yellowstone River significantly more than expected by chance. Fort Peck Dam has altered the hydrograph, thermal regime, and sediment and organic matter transport in the upper Missouri River ecosystem. These conditions may reduce this reach's suitability for pallid and shovelnose sturgeon in a variety of ways, including disrupted exogenous movement cues, altered river morphology (Kellerhals and Church 1989), organic matter transport, and faunal assemblages (Vannote et al. 1980). Riparian plant communities may be altered (Johnson 1993), causing a reduction of snag recruitment (Hesse and Mestl 1993), which is important for production of aquatic invertebrates in sandy rivers (Benke et al. 1984). Moreover, reduced floodplain connectivity may diminish food production in large river-floodplain ecosystems (Junk et al. 1989). Fort Peck Dam has also shifted turbidity, substrate, and temperature conditions towards conditions more typical of river reaches that are upstream (Ward and Stanford 1983) of the pallid sturgeon's native range (Lee et al. 1980; Dryer and Sandvol 1993). Because Missouri River fishes have evolved under conditions of high natural turbidity (Pflieger and Grace 1987) reduction of turbidity may favor visually oriented nonnative species.

Implications for Recovery of Pallid Sturgeon

Free-flowing, sandy, diverse, and dynamic riverine habitats were most used by pallid sturgeon. The lower Yellowstone River and the Missouri River BTC is virtually the only habitat of this character remaining in the range of the pallid sturgeon, and as such represents essential habitat. However, the apparent lack of recruitment to this population (Dryer and Sandvol 1993) suggests that this existing habitat may not be sufficient for production of all life stages, or recovery of pallid sturgeon. The Missouri River from the confluence upstream to Fort Peck Dam and Lake Sakakawea, which inundates former riverine habitat, appear to be largely unsuitable as habitat for pallid sturgeon at present. Restoration of these habitats to conditions capable of producing and sustaining pallid sturgeon will probably require reestablishing historical ecological conditions and processes such as hydrological and thermal regimes and sediment transport. The long-range movements of pallid sturgeon we observed, coupled with the insularization of their habitat through dam construction and channelization, also lead to concerns within the framework of metapopulation dynamics (Hanski and Gilpin 1991), lending support to the idea that connectivity between existing pallid sturgeon subpopulations may need to be restored (Dryer and Sandvol 1993).

Acknowledgments

Funding for this study was provided by Division of Cooperative Units, National Biological Service, U. S. Fish and Wildlife Service (USFWS) Ecological Services offices in Helena, Montana, and Bismarck, North Dakota, and USFWS Denver Regional Office. P. Clancey of Montana Fish, Wildlife and Parks (FWP) initiated telemetry of pallid and shovelnose sturgeon in this study area in 1989, and FWP biologist A. Tews continued with the research beginning in 1992. A. Tews, P. Clancey, and S. Krentz, and A. Sandvol USFWS Office of Ecological Services in Bismarck, North Dakota, captured sturgeons for this study. We thank P. Munholland and J. Borkowski for statistical advice. D. Gustafson performed computer programming. We thank P. Stewart of FWP for loan of a boat. M. Baxter, C. Endicott, D. Gustafson, E. Jeans, S. Lohr, D. Megargle, J. J. Piccolo, D. Venditti, and J. Zelenak assisted in the field. D. Galat, W. Gardner, C. Kaya, S. Krentz, A. Tews, M. Quist, and A. Zale provided helpful comments on an earlier draft. Trade names are mentioned solely for information. No endorsement is implied.

References

Adams, S. R., G. R. Parsons, J. J. Hoover, and K. J. Killgore. 1997. Observations of swimming ability in shovelnose sturgeon (*Scaphirhynchus platorynchus*). Journal of Freshwater Ecology 12:631–633.

Allan, J. D. 1995. Stream ecology: structure and function of running waters. Chapman and Hall, London.

Alldredge, J. R., and J. T. Ratti. 1992. Further comparison of some statistical techniques for analysis of resource selection. Journal of Wildlife Management 56:1–9.

Apperson, K. A., and P. J. Anders. 1990. Kootenai River white sturgeon investigations and experimental culture. Annual Progress Report FY 1989 to Bonneville Power Administration, Portland, Oregon.

Backes, K. M., W. M. Gardner, D. Scarnecchia, and P. A. Stewart. 1994. Lower Yellowstone River pallid sturgeon study IV and Missouri River pallid sturgeon creel survey. Montana Department of Fish, Wildlife, and Parks, Miles City.

Bailey, R. M., and F. B. Cross. 1954. River sturgeons of the American genus *Scaphirhynchus*: characters, distribution, and synonomy. Papers of the Michigan Academy of Science, Arts, and Letters 39:169–209.

Barnickol, P. G., and W. C. Starret. 1951. Commercial and sport fishes of the Mississippi River between Caruthersville, Missouri, and Dubuque, Iowa. Illinois Natural History Survey Bulletin 25:267–350.

Benke, A. C., T. C. Van Arsdall, Jr., D. M. Gillespie, and F. K. Parrish. 1984. Invertebrate productivity of a subtropical blackwater river: the importance of habitat and life history. Ecological Monographs 54: 25–63.

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.

Brown, C. J. D. 1955. A record-size pallid sturgeon, *Scaphirhynchus albus*, from Montana. Copeia 1955: 55.

Brown, C. J. D. 1971. Fishes of Montana. Big Sky Books, Bozeman, Montana.

Carlson, D. M., W. L. Pflieger, L. Trial, and P. S. Haverland. 1985. Distribution, biology, and hybridization of *Scaphirhynchus albus* and *Scaphirhynchus platorynchus* in the Missouri and Mississippi rivers. Environmental Biology of Fishes 14:51–59.

Christenson, L. M. 1975. The shovelnose sturgeon, *Scaphirhynchus platorynchus* (Rafinesque) in the Red Cedar–Chippewa River system, Wisconsin. Wisconsin Department of Natural Resources Research Report 82, Madison.

Cross, F. B. 1967. Handbook of fishes in Kansas. University of Kansas Museum of Natural History Miscellaneous Publication 45, Lawrence.

Curtis, G. L. 1990. Habitat use by shovelnose sturgeon in pool 13, upper Mississippi River, Iowa. Master's thesis. Iowa State University, Ames.

Curtis, G. L., J. S. Ramsey, and D. L. Scarnecchia. 1997. Habitat use and movements of shovelnose sturgeon in Pool 13 of the upper Mississippi River during extreme low flow conditions. Environmental Biology of Fishes 50:175−182.

Dryer, M. P., and A. J. Sandvol. 1993. Pallid sturgeon recovery plan. U.S. Fish and Wildlife Service, Bismarck, North Dakota.

Erickson, J. D. 1992. Habitat selection and movement of pallid sturgeon in Lake Sharpe, South Dakota. Master's thesis. South Dakota State University, Brookings.

Forbes, S. A., and R. E. Richardson. 1905. On a new shovelnose sturgeon from the Mississippi River. Bulletin of the Illinois State Laboratory of Natural History 7:35–47.

Funk, J. L., and J. W. Robinson. 1974. Changes in the channel of the lower Missouri River and effects on fish and wildlife. Missouri Department of Conservation, Aquatic Series 11, Jefferson City.

Gardner, W. M. 1994. Missouri River pallid sturgeon inventory. Montana Department of Fish, Wildlife, and Parks, Federal Aid in Sport Fish Restoration, Project F-46-R-7, Final Report, Helena.

Gardner, W. M. 1995. The status of the pallid sturgeon population in the upper Missouri River. Pages 85–93 *in* Proceedings of the first joint meeting of the Montana/North Dakota Pallid Workgroup and the Fluvial Arctic Grayling Workgroup. Montana Department of Fish, Wildlife, and Parks, Helena.

Gardner, W. M., and P. Stewart. 1987. The fishery of the Lower Missouri River, Montana. Montana Department of Fish, Wildlife, and Parks, Federal Aid in Sport Fish Restoration, Project F-46-R-5, Study 3, Final Report, Helena.

Gilbraith, D. M., M. J. Schwalbach, and C. R. Berry. 1988. Preliminary report on the status of the pallid sturgeon, *Scaphirhynchus albus,* a candidate endangered species. South Dakota Cooperative Fish and Wildlife Research Unit, Department of Wildlife and Fisheries Sciences, South Dakota State University, Brookings.

Hamilton, K., and E. P. Bergersen. 1984. Methods to estimate aquatic habitat variables. U.S. Bureau of Reclamation, Engineering and Research Center, Denver, Colorado.

Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain. Biological Journal of the Linnean Society 42:3–16.

Held, J. W. 1969. Some early summer foods of the shovelnose sturgeon in the Missouri River. Transactions of the American Fisheries Society 98:514–517.

Helms, D. 1974. Shovelnose sturgeon in the Mississippi River, Iowa. Iowa Conservation Commission, Fisheries Research Technical Series 74-3, Des Moines.

Hesse, L. W. 1987. Taming the wild Missouri River: what has it cost? Fisheries 12(2):2–9.

Hesse, L. W. 1994. The status of Nebraska fishes in the Missouri River, 5. Selected chubs and minnows (Cyprinidae): sicklefin chub (*Macrhybopsis meeki*), sturgeon chub (*M. gelida*), silver chub (*M. storeriana*), speckled chub (*M. aestivalis*), flathead chub (*Platygobio gracilis*), plains minnow (*Hybognathus placitis*), and western silvery minnow (*H. argyritis*). Transactions of the Nebraska Academy of Sciences 21:99–108.

Hesse, L. W., and G. E. Mestl. 1993. An alternative hydrograph for the Missouri River based on precontrol condition. North American Journal of Fisheries Management 13:360–366.

Hesse, L. W., and W. Sheets. 1993. The Missouri River hydrosystem. Fisheries 18(5):5–14.

Hoopes, D. T. 1960. Utilization of mayflies and caddisflies by some Mississippi River fishes. Transactions of the American Fisheries Society 89:32–34.

Hurley, S. T., W. A. Hubert, and J. G. Nickum. 1987. Habitats and movements of shovelnose sturgeons in the upper Mississippi River. Transactions of the American Fisheries Society 116:655–662.

Hynes, H. B. N. 1970. The ecology of running waters. University of Toronto Press, Toronto.

Johnson, W. C. 1993. Divergent response of riparian vegetation to flow regulation on the Missouri and Platte rivers. U.S. National Biological Survey Biological Report 19:426–431.

Junk, W. J., P. B. Bailey, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. Proceedings of the international large river symposium. Canadian Special Publication of Fisheries and Aquatic Sciences 106:110–127.

Kallemeyn, L. W. 1983. Status of the pallid sturgeon (*Scaphirhynchus albus*). Fisheries 8(1):3–9.

Karr, J. R. 1991. Biological integrity: a long-neglected aspect of water resource management. Ecological Applications 1:66–84.

Keenlyne, K. D. 1989. A report on the pallid sturgeon. U.S. Fish and Wildlife Service, Pierre, South Dakota.

Keenlyne, K. D. 1997. Life history and status of the shovelnose sturgeon, *Scaphirhynchus platorynchus.* Environmental Biology of Fishes 48:291–298.

Keenlyne, K. D., C. J. Henry, A. Tews, and P. Clancey. 1994. Morphometric comparisons of Upper Missouri River sturgeons. Transactions of the American Fisheries Society 123:779–785.

Keenlyne, K. D., and L. G. Jenkins. 1993. Age at sexual maturity of the pallid sturgeon. Transactions of the American Fisheries Society 122:393–396.

Kellerhals, R., and M. Church. 1989. The morphology of large rivers: characterization and management. Proceedings of the international large river symposium. Canadian Special Publication of Fisheries and Aquatic Sciences 106:31–48.

Kellerhals, R., M. Church, and D. I. Bray. 1976. Classification and analysis of river processes. Proceedings of the American Society of Civil Engineers, Journal of Hydraulics Division 102(July):813–829.

Koch, R., R. Curry, and M. Weber. 1977. The effect of altered streamflow on the hydrology and geomorphology of the Yellowstone River basin, Montana. Montana Department of Natural Resources and Conservation, Technical Report 2, Helena.

Krentz, S. 1994. Observations and findings of the Missouri River Fish and Wildlife Assistance Office. U.S. Fish and Wildlife Service, Missouri River Fish and Wildlife Management Assistance Office, Bismarck, North Dakota.

Latka, C., J. Nestler, and L. W. Hesse. 1993. Restoring physical habitat in the Missouri River: a historical perspective. U.S. National Biological Survey Biological Report 19:350–359.

Lee, D. S., C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister, and J. R. Stauffer, Jr. 1980. Atlas of North American freshwater fishes. North Carolina State Museum of Natural History, Raleigh.

Megargle, D. 1997. Temporal variation in diet and food selection of shovelnose sturgeon in the Missouri River above Fort Peck Reservoir, Montana. Master's thesis. Montana State University, Bozeman.

Modde, T., and J. C. Schmulbach. 1977. Food and feeding behavior of the shovelnose sturgeon, *Scaphirhynchus platorynchus,* in the unchannelized Missouri River, South Dakota. Transactions of the American Fisheries Society 116:655–662.

Moos, R. E. 1978. Movement and reproduction of shovelnose sturgeon *Scaphirhynchus platorynchus,* in the Missouri River, South Dakota. Doctoral dissertation. University of South Dakota, Vermillion.

Neter, J., W. Wasserman, and G. A. Whitmore. 1993. Applied statistics. Allyn and Bacon, Boston.

Nue, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. Journal of Wildlife Management 38:541–545.

Pflieger, W. L. 1975. Fishes of Missouri. Missouri Department of Conservation, Jefferson City.

Pflieger, W. L., and T. B. Grace. 1987. Changes in the fish fauna of the Lower Missouri River, 1940−1983. Pages 166–177 *in* W. J. Matthews and D. C. Heins, editors. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

Phelps, S. R., and F. W. Allendorf. 1983. Genetic identity of pallid and shovelnose sturgeon. Copeia 1983: 696–700.

Quist, M. C., and C. S. Guy. 1999. Spatial variation in population characteristics of shovelnose sturgeon in the Kansas River. Prairie Naturalist 31:65–74.

Quist, M. C., J. S. Tillma, M. N. Burlingame, and C. S. Guy. 1999. Overwinter habitat use of shovelnose sturgeon in the Kansas River. Transactions of the American Fisheries Society 128:522–527.

Ross, M. J. 1981. Shielded-needle technique for surgically implanting radio-frequency transmitters in fish. Progressive Fish-Culturist 44:41–43.

Schmulbach, J. C. 1974. An ecological study of the Missouri River prior to channelization. University of South Dakota, Completion Report, Project B-024-S, Vermillion.

Shields, R. R., M. K. White, T. M. Brosten, and C. L. Chambers. 1994. Water resources data, Montana water year 1993. U.S. Geological Survey, Water Data Report MT-93-1, Washington, D.C.

Stalnaker, C. B., R. T. Milhous, and K. D. Bovee. 1989. Hydrology and hydraulics applied to fishery management in large rivers. Canadian Special Publication of Fisheries and Aquatic Sciences 106:13–30.

Stewart, P. A. 1995. Effect of intake diversion dam on the pallid and shovelnose sturgeon in the lower Yellowstone River. Pages 94–99 *in* Proceedings of the first joint meeting of the Montana/North Dakota Pallid Workgroup and the Fluvial Arctic Grayling Workgroup. Montana Department of Fish, Wildlife, and Parks, Helena.

Tews, A. 1994. Pallid sturgeon and shovelnose sturgeon in the Missouri River from Fort Peck Dam to Lake Sakakawea and in the Yellowstone from intake to its mouth. Montana Department of Fish, Wildlife, and Parks, Final Report, Helena.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

Ward, J. V., and J. A. Stanford. 1983. The serial discontinuity concept of lotic ecosystems. Pages 29–42 *in* T. D. Fontaine and S. M. Bartell, editors. Dynamics of lotic ecosystems. Ann Arbor Science, Ann Arbor, Michigan.

Watson, J. H., and P. A. Stewart. 1991. Lower Yellowstone River pallid sturgeon study. Montana Department of Fish, Wildlife, and Parks, Miles City.

White, G. C., and R. A. Garrott. 1992. 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. Proceeding of the symposium on restoration planning for the rivers of the Mississippi River ecosystem. U.S. National Biological Survey Biological Report 19:396–414.

Winter, J. 1996. Advances in underwater biotelemetry. Pages 555–590 *in* B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

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