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Keith L. Hurley

Nebraska Game and Parks Commission

Robert J. Sheehan

Southern Illinois University Carbondale

Roy C. Heidinger

Southern Illinois University Carbondale

Paul S. Wills

Southern Illinois University Carbondale

Bob Clevensine

U.S. Fish and Wildlife Service

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Habitat Use by Middle Mississippi River Pallid Sturgeon

KEITH L. HURLEY*

Nebraska Game and Parks Commission,
2200 North 33rd Street, Lincoln, Nebraska 68503-0370, USA

ROBERT J. SHEEHAN, ROY C. HEIDINGER, AND PAUL S. WILLS

Fisheries and Illinois Aquaculture Center and Department of Zoology,
Southern Illinois University, Carbondale, Illinois 62901-6511, USA

BOB CLEVENSTINE

U.S. Fish and Wildlife Service,
4469 48th Avenue Court, Rock Island, Illinois 61201, USA

Abstract.—Little is known about the habitat preferences and needs of pallid sturgeon *Scaphirhynchus albus*, which was federally listed as endangered in 1990. To learn more about habitat use and selection by pallid sturgeon, sonic transmitters were surgically implanted in 27 individuals from the middle Mississippi River. Study fish were located 184 times (1–23 times/individual) from November 1995 to December 1999. Of the seven macrohabitats identified, pallid sturgeon were found most often in main-channel habitats (39% of all relocations) and main-channel border habitats (26%); the between-wing-dam habitats were used less often (14%). Strauss's linear selectivity index (L_i) values indicated that study fish exhibited positive selection for the main-channel border, downstream island tips, between-wing-dam, and wing-dam-tip habitats; they showed negative selection for main-channel, downstream of wing dams, and upstream of wing dam habitats. Comparison of L_i values for four temperature ranges and three daily mean discharge ranges revealed little change in habitat selection due to temperature or discharge. Habitat use patterns also were similar across seasons and discharge regimes, except during spring months when between-wing-dam habitats saw greater use and main-channel and main-channel border habitat use declined. These changes may have been a response to high river stages associated with spring flooding, which may create favorable feeding areas in the between-wing-dam habitats. Enhancement and restoration of habitat diversity, particularly downstream island tip and between-wing-dam habitats, may be necessary for the recovery of pallid sturgeon in the middle Mississippi River.

The pallid sturgeon *Scaphirhynchus albus* is one of three river sturgeons of the genus *Scaphirhynchus* that is endemic to North America. Bailey and Cross (1954) characterized the pallid sturgeon as “nowhere common.” Pallid sturgeon numbers have since decline markedly (Kallemeyn 1983; Carlson et al. 1985; Dryer and Sandvol 1993), resulting in the species being federally listed as endangered in 1990. Management of pallid sturgeon populations has been hindered by the lack of scientific information about their life history and habitat requirements (Kallemeyn 1983). This lack of biological information was identified by the Pallid Sturgeon Recovery Plan (Dryer and Sandvol 1993), and the scientific investigation of the life history and habitat needs of all life stages of the species was included in plan's objectives (Dryer and Sandvol 1993). A 1997 survey of biologists

working on North American sturgeon and paddlefish, also noted a lack of knowledge about the biology and life history of the pallid sturgeon and a need for additional research (Beamesderfer and Farr 1997).

The primary macrohabitat of pallid sturgeon is reported to be the main channels of the Missouri and Mississippi rivers and their largest tributaries (Bailey and Cross 1954; Carlson and Pflieger 1981; Erickson 1992); pallid sturgeon were not found in backwater areas, submerged islands, or riparian areas (Erickson 1992). Little is known about the microhabitat needs of pallid sturgeon and almost no quantitative data are available on its habitat use (Bramblett and White 2001). Bramblett and White (2001) identified individual home ranges for pallid sturgeon of up to 250 km. Large home ranges such as this increase the difficulty of identifying microhabitat needs beyond general habitat use.

Modification of the middle Mississippi River to maintain a 2.7-m navigation channel has resulted

* Corresponding author: khurley@ngpc.state.ne.us

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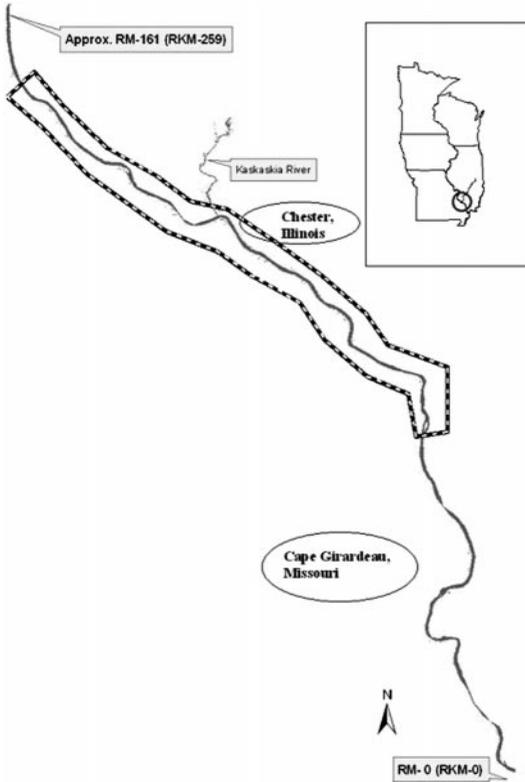


FIGURE 1.—Study area of the middle Mississippi River in which pallid sturgeon were radio-tagged; the area within the dotted outline is the area that received the most telemetry effort.

in longitudinal and cross-sectional changes in channel morphometry. These changes are suspected to have reduced habitat diversity, availability, and value for large river organisms, including the pallid sturgeon. The Pallid Sturgeon Recovery Plan suggested that destruction and alteration of habitats by human modification were the primary threat to the species. However, these modifications have continued under a federal program to operate and maintain the navigation system. Information on habitat use and selection is

necessary to evaluate the effect of this program on pallid sturgeon and to suggest modifications to support recovery of the species. The goal of this study was to examine the habitat use and selection of adult sturgeon in the middle Mississippi River. The middle Mississippi River stretches 314 km from the mouth of the Missouri River near St. Louis, Missouri, to the mouth of the Ohio River near Cairo, Illinois (Figure 1). This region of the river is highly channelized and has few secondary or abandoned channels, sandbars, or islands. The Pallid Sturgeon Recovery Plan identified the middle Mississippi River as a recovery-priority area (Dryer and Sandvol 1993).

Methods

Pallid sturgeon were obtained from commercial fishers, the Missouri Department of Conservation, and by sampling conducted by Southern Illinois University at Carbondale (SIUC). Character index (CI) values (Wills et al. 2002) were calculated to quantify the strength of the pallid sturgeon characteristics exhibited by the fish. Character index values with increasingly negative numbers represent fish with stronger pallid sturgeon characteristics, whereas increasingly positive numbers represent fish with stronger shovelnose characteristics.

Sonic transmitters were surgically implanted into their body cavity, and study fish were released as close to their capture site as logistically possible. Transmitters used for the study (18 mm in diameter, 90 mm long, and weighing 12 g) transmitted at 40 kHz, were uniquely pulse-coded, and had an estimated life of 13 months. Fish were located with a Sonotronics USR-91 receiver with a dual hydrophone array. Location coordinates were then taken using a differential global positioning system, and the position was recorded on U.S. Army Corps of Engineers navigation charts. Macrohabitat type was determined from a list of habitat classifications (Table 1; Figure 2) in reference to habitat structures such as islands, channels,

TABLE 1.—Standard distances used in delineating borders between different middle Mississippi River macrohabitats used in habitat availability analysis for pallid sturgeon.

Habitat	Standards for delineation
Wing dam upstream	74.9 m upstream and inside of tip of wing dam
Wing dam downstream	170.9 m downstream and inside of tip of wing dam
Wing dam tip	43.8-m radius around tip of wing dam
Between wing dams	All area between and inside tips of consecutive wing dams not otherwise delineated
Downstream island tip	163.6-m radius around downstream tip of islands
Main-channel border	253.2 m from shore lacking wing dams
Main channel	All area not otherwise delineated

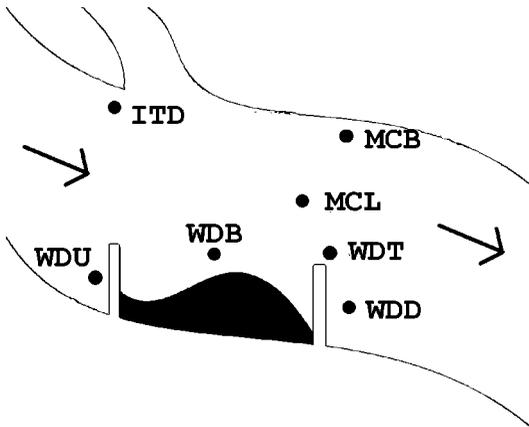


FIGURE 2.—Schematic of macrohabitat classifications of areas where radio-tracking effort for pallid sturgeon was focused. Abbreviations are as follows: MCL = main channel, MCB = main-channel border, WDU = wing dam upstream, WDD = wing dam downstream, WDT = wing dam tip, WDB = between wing dams, and ITD = downstream island tip.

shorelines, and wing dams (i.e., jetty-like rock structures extending laterally from the shore into the river that are used to redirect current from the shoreline to the main channel). These habitat classifications included main channel (MCL), main-channel border (MCB; i.e., any associated shoreline lacking current-obstructing features), immediate upstream of a wing dam (WDU), immediate downstream of a wing dam (WDD), the wing dam tip (WDT), between two consecutive wing dams (WDB), and the downstream side of an island tip (ITD).

Macrohabitat associations were expressed as a percentage of total relocations per habitat type. Additionally, habitat associations were characterized according to surface water temperature at point of relocation. Surface water temperature at point of contact was used to separate macrohabitat associations into four groups: less than 4°C, 4°C to 10°C, 10°C to 20°C (during both spring and fall months), and greater than 20°C. Increased mortality and decreased swimming ability have been shown in some fishes at temperatures below 4°C (Sheehan et al. 1990; Bodensteiner and Lewis 1992). The other temperature ranges were chosen to represent the remainder of the winter season, spring and fall, and summer, respectively.

Habitat availability data were obtained from U.S. Army Corps of Engineers navigation charts. Twenty, 1.6-km stretches were randomly chosen from the river stretch occupied by the study fish.

To ensure up-to-date accuracy the navigation charts of these 20 stretches were ground-truthed (i.e., physical examination of each 1.6-km stretch to determine whether the habitats shown on the charts had been modified, added, or removed). Changes typically included the addition or removal of wing dams and the disappearance of small islands, presumably due to erosional processes. Changes were then corrected on the navigation charts, and charts were then enlarged to a scale of 89 mm = 914.4 m.

Each occurrence of a macrohabitat type in the 1.6-km stretch was outlined according to a pre-defined set of standards (Table 1). These standards were derived from a mean of field measurements of representative habitat types via a prismatic rangefinder. Three different sites of each macrohabitat were arbitrarily selected; at three arbitrary locations at each site, two measurements were taken from the edge of that particular habitat feature. The delineated areas on the charts were then measured three times using a planimeter and averaged. Results were summed by macrohabitat type, and the percentage of all available habitats was calculated for each macrohabitat. Strauss's (1979) linear selectivity index (L_i) was chosen to examine habitat selection by pallid sturgeon because it is not as susceptible to sampling bias when the habitat type represents a small or minute proportion of all available habitats (Lechowicz 1982). A chi-square goodness-of-fit test was used to determine whether significant selection was occurring. To determine direction of selection for each habitat, L_i values were graphed with their 95% confidence intervals.

To examine the effects of temperature, L_i values were calculated for each habitat for the four temperature ranges (0–4°C, 4–10°C, 10–20°C, and >20°C). A chi-square goodness-of-fit test was used to determine whether significant selection was occurring within each temperature range. To examine changes in selection for individual habitats due to temperature, L_i values were grouped by temperature and habitat and graphed with their 95% confidence intervals.

To examine the effects of discharge, L_i index values were calculated for each habitat for three daily mean discharge ranges: low (0–4,669 m³/s), medium (4,670–7,641 m³/s), and high (>7,641 m³/s). These break points correspond to the 33.3% and 66.6% daily mean discharge for all days during the sampling period (Figure 3). All discharge data were obtained from the U.S. Geological Survey for the Chester, Illinois, gauging station at river kilometer

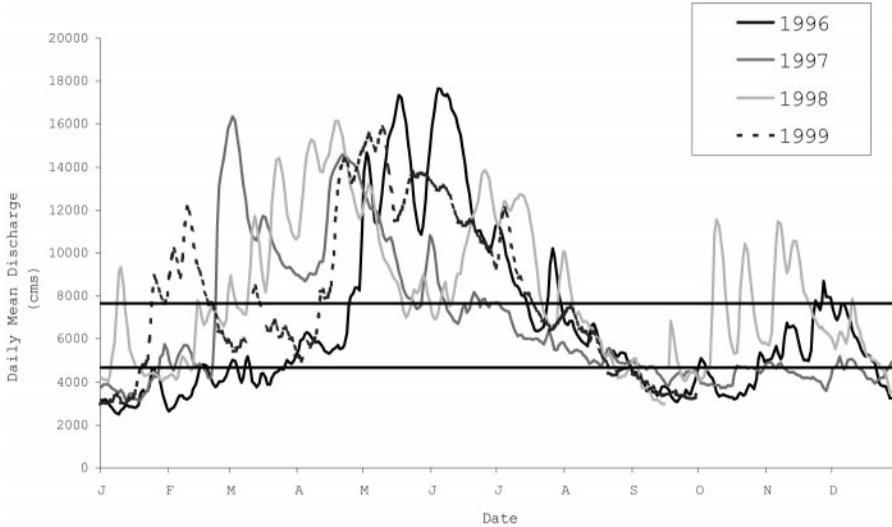


FIGURE 3.—Daily mean discharge values (m³/s) obtained from the U.S. Geological Survey for the Chester, Illinois, gauging station on the Mississippi River from January 1, 1996, through September 30, 1999. Months are abbreviated by their first letters; the solid horizontal lines represent the break points between the low-, middle-, and high-discharge regimes.

177. A chi-square goodness-of-fit test was used to determine if significant selection was occurring within each discharge range. To examine changes in selection for individual habitats due to discharge, L_i values were grouped by discharge range and hab-

itat and graphed with their 95% confidence intervals.

Results

Twenty pallid sturgeon (614–888 mm standard length, 950–3,273 g) were surgically implanted with ultrasonic transmitters between November 1995 and December 1999. Percent weight of transmitters to body weight ranged from 0.4% to 1.3%. Character index values ranged from +0.1345 to –2.08. Although 6 of the 27 sturgeon exhibited characteristics of hybrid sturgeon, all but one of the CI values fell into the range that Carlson and Pflieger (1981) identified as pallid sturgeon, and all 27 values were below CI values of shovelnose sturgeon collected from the middle Mississippi River. Character index values for the radio-tagged fish were similar to those for other pallid sturgeon captured during the study period but not radio-tagged due to their small size or other considerations.

A total of 184 locations of study fish were made between November 1995 and December 1999. These 184 contacts were all made during daytime hours. Individual fish were located 1 to 23 times (Table 2). Approximately 4,273 km of tracking effort was exerted during the 3 years of this study. To maximize contact with the study fish, tracking effort was mostly focused between river kilometers 130 and 243 (Figure 4) because that was the

TABLE 2.—Number of locations and days at large for pallid sturgeon implanted with sonic transmitters and released into the middle Mississippi River. Number of locations does not include initial capture or release location. Days at large is the time from date of release to date of last location.

Transmitter number	Number of locations	Days at large
7–8	1	5
2,273	1	20
239	1	8
276	1	24
456	2	43
5–10	2	200
3,334	3	263
339	5	106
2,264	6	337
384	6	217
2,237	8	588
348	9	170
465	10	228
375	12	395
267	15	519
2,588	18	417
366	19	1,488
294	20	499
249	22	527
357	23	506

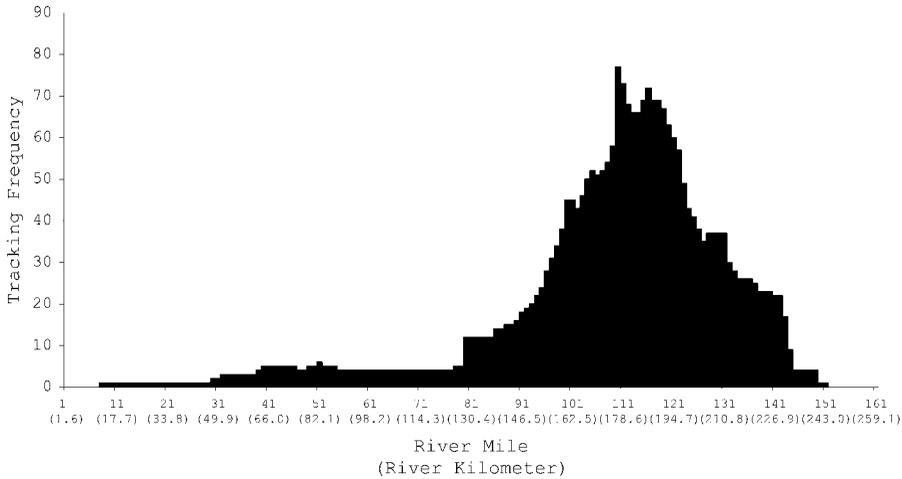


FIGURE 4.—Tracking frequency (the total number of days that a given river kilometer was radio-tracked divided by the total radio-tracking days conducted to locate radio-tagged pallid sturgeon in the middle Mississippi River), November 1995 to December 1999.

portion of the study area where fish were located most often. However, effort was also expended in other parts of the study area in attempts to find missing study fish.

Study sturgeon were located in MCL habitats 39% of the time. The MCB and WDB habitats made up 26% and 14% of all contacts, respectively (Table 3). Habitat associations for the winter season were broken down into two different temperature ranges: less than 4°C, and 4–10°C. At less than 4°C the study sturgeon were found in association with current-disrupting habitat features such as the ITD (12%) and WDD (10%) than at other times during the study. However, the MCL (49%) was still used most often. The diversity of habitat associations at less than 4°C were similar

to other seasons, six of the seven habitats being used. Once winter temperatures rose above 4°C, habitat use became more restricted. The MCL (54%) and the MCB (28%) together composed 82% of all relocations in this temperature range.

Habitat associations during the spring months (10–20°C) deviated from those found during the rest of the year. The MCL habitat, which was used heavily during the rest of the year, contributed only 11% of the locations during spring, whereas spring use of the WDB habitats increased greatly (36%). It is notable, however, that the number of contacts during spring was low ($N = 19$) because of difficulties in detecting fish during spring flooding. During fall months at the same temperatures, habitat associations were similar to those during the

TABLE 3.—Percentage occurrence and, in parentheses, number of pallid sturgeon occurrences or locations in each macrohabitat, by season (based on temperature) and relative availability of each habitat type within the middle Mississippi River study area (river kilometers 1.6 to 265.7), November 1995 to September 1998. Abbreviations are as follows: MCL = main channel, MCB = main-channel border, WDD = wing dam downstream, WDB = between wing dams, WDU = wing dam upstream, WDT = wing dam tip, and ITD = downstream island tip.

Habitat type	Percent of available habitat	Percent occurrence (number of locations)					
		All seasons	Extreme winter (<4°C)	Winter (≥4 to <10°C)	Spring (≥10 to <20°C)	Fall (≥10 to <20°C)	Summer (≥20°C)
MCL	64	39 (73)	49 (21)	54 (17)	11 (2)	56 (16)	27 (17)
MCB	11	26 (48)	14 (6)	28 (9)	26 (5)	28 (8)	32 (20)
WDD	9	4 (7)	10 (4)	3 (1)	11 (2)	0 (0)	0 (0)
WDB	8	14 (25)	10 (4)	9 (3)	36 (7)	3 (1)	16 (10)
WDU	4	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	2 (1)
WDT	3	7 (13)	5 (2)	0 (0)	0 (0)	10 (3)	13 (8)
ITD	1	9 (17)	12 (5)	6 (2)	16 (3)	3 (1)	10 (6)
Total N		184	42	32	19	29	62

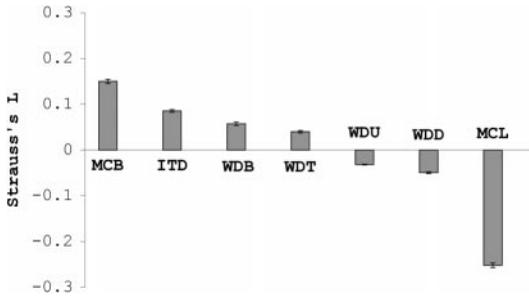


FIGURE 5.—Strauss's (1979) linear selectivity index (L_i) values for each macrohabitat radio-tracked for pallid sturgeon use in the middle Mississippi River. Positive values represent positive selection, negative values negative selection; error bars represent 95% confidence intervals. Abbreviations are given in the caption to Figure 2.

rest of the year. The MCL contributed 56% of the fall contacts and the MCB contributed 28%, totaling 84% of the contacts for these two habitat types (Table 3).

Summer (surface water temperatures $>20^{\circ}\text{C}$) habitat associations were diverse and closely resembled the overall habitat associations (Table 3). The use of WDT macrohabitats was heavier during the summer months than during other seasons.

Habitat availability analysis indicated that the study area was approximately 64% MCL and 11% MCB. The ITD habitat contributed the smallest amount of the study area at only 1%. The other macrohabitat types, WDD, WDB, WDU, and WDT, contributed 9%, 8%, 4%, and 3%, respectively (Table 3).

The L_i ranged from -0.22 to $+0.15$ (Figure 5). A chi-square goodness-of-fit test indicated that the distribution of habitat use differed significantly from habitat availability ($\chi^2 = 154.90$, critical value with 6 df = 12.59). Radio-tagged sturgeon

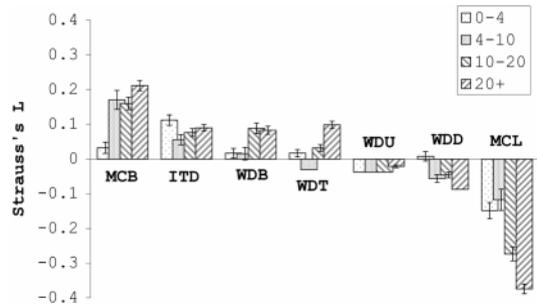


FIGURE 6.—Strauss's (1979) linear selectivity index (L_i) values by temperature regime ($^{\circ}\text{C}$; four categories) for each macrohabitat radio-tracked for pallid sturgeon use in the middle Mississippi River. See the caption to Figure 5 for additional information.

showed decreasingly positive selection for MCB, ITD, WDB, and WDT habitats; they exhibited increasingly negative selection for MCL, WDD, WDU (Figure 5).

Chi-square goodness-of-fit tests indicated that significant habitat selection was occurring within temperature ranges (Table 4). However, only two habitats showed a change from positive to negative selection, or vice versa across temperatures. The WDT habitats were positively selected for during each temperature range except 4–10 $^{\circ}\text{C}$ (Figure 6).

A chi-square goodness-of-fit test indicated that the distribution of habitat use was significantly different from the habitat availability at the low, medium, and high discharge regimes (Table 4). Selection direction did not change for any habitat across discharge regimes (Figure 7).

Discussion

In the context of this study, the term “habitat use” refers to the habitats with which the study

TABLE 4.—Chi-square goodness-of-fit results of Strauss's linear selectivity index values for pallid sturgeon habitat selection in the middle Mississippi River, by temperature range and discharge range. Low, medium, and high discharge ranges were 0–4,669; 4,670–7,641; and greater than 7,641 m^3/s , respectively. A χ^2 value greater than 12.59 indicates that significant selection occurred at $\alpha = 0.05$, df = 6.

Variable	Range	χ^2
Temperature ($^{\circ}\text{C}$)	0–4	187.96
	4–10	33.95
	10–20	230.80
	>20	194.99
Discharge	Low	99.08
	Medium	102.58
	High	297.18

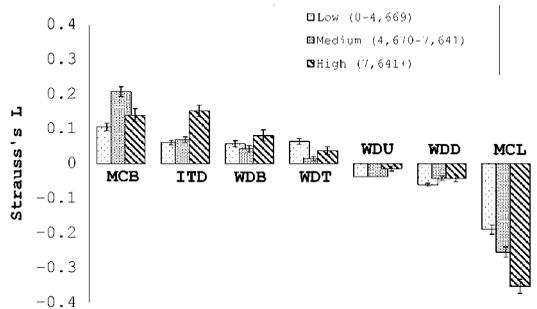


FIGURE 7.—Strauss's (1979) linear selectivity index (L_i) values by discharge regime (m^3/s) for each macrohabitat radio-tracked for pallid sturgeon use in the middle Mississippi River. See the caption to Figure 5 for additional information.

sturgeon were associated. High-use areas are important to pallid sturgeon because these are the habitats where they were most commonly found. Water-use changes or habitat modifications in these areas need to be carefully examined for their effects on pallid sturgeon. Habitat selection takes into account the availability of the habitat and compares that availability with the amount of use each habitat receives. Habitats that are negatively selected may represent areas that are undesired, unavailable, or simply used less frequently. Habitats that are positively selected may represent areas preferred by or important to pallid sturgeon and may represent the types of habitat that should be created, maintained, and protected for the benefit and recovery of the species.

Radio-tagged fish were found most often in the MCL habitat, followed by MCB and WDB habitats. However, MCB, ITD, BWD, and WDT were important areas of positive habitat selection. These areas would seem to be preferred by middle Mississippi River pallid sturgeon and may represent important pallid sturgeon habitat. Bramblett and White (2001) found that pallid sturgeon were more often located in reaches with diverse habitats, channels, and islands rather than single, uniform channels.

Although the radio-tagged sturgeon were found most often in the MCL, they exhibited stronger negative selection for MCL than for any other habitat. This is not surprising considering the MCL contributed 64% of available habitat. The MCL habitat would seem to be an area where pallid sturgeon are commonly found, yet it may not be a preferred habitat for the species. This may be explained by the fact that movement among different macrohabitat types would dictate movement through MCL habitats. Snook et al. (2002) never found sturgeon directly in the channel of the Platte River but often adjacent to it, along transitions from shallower, sandbar habitats. Similarly, pallid sturgeon in the middle Mississippi River during our study showed high use of MCB areas and positive selection for main-channel borders and ITD habitats.

The ITD represented less than 1% of the habitat available in the middle Mississippi River. Although this is not a common habitat, the radio-tagged fish did seem to positively select this area. Bramblett and White (2001) found that pallid sturgeon in the upper Missouri and lower Yellowstone rivers preferred reaches with a high density of islands and suggested these reaches provided better availability of prey fishes and invertebrates. Snook

et al. (2002) found pallid sturgeon to be associated with the sharp change in depths and transition areas between the downstream edges of sandbars and the main channel of the Platte River. Snook et al. (2002) noted that these areas were often just downstream from habitats that were ideally suited for a number of small prey species of fish. In the middle Mississippi River flows cut away at the rich embankments of side channels releasing benthic macroinvertebrates that are swept back to the main stem in the ITD habitats. Macroinvertebrates were found to contribute a large part of pallid sturgeon diets (Carlson et al. 1985). Sturgeon may use these habitats as breakwater structures that provide lower water velocities that facilitates feeding on invertebrates and small fish being swept out of the side channels.

Temperature and water velocity are two environmental factors that greatly affect behavior and habitat use of many riverine fishes. Extreme winter water temperatures ($<4^{\circ}\text{C}$) can severely affect swimming ability and mortality of riverine fishes (Sheehan et al. 1990). Habitat associations during winter (water temperature $<4^{\circ}\text{C}$) did not differ from those found during the rest of the year. Habitat associations also were as diverse as those during any other season, the radio-tagged fish being found in six different habitats. Likewise, no shifts between habitat selection and avoidance were noticed during these temperatures, so it appears that winter temperatures did not have an effect on habitat selection and use.

In fact, habitat use and selection by pallid sturgeon did not seem to be affected by any temperature or discharge regime in the middle Mississippi River, except for spring months when the temperature ranged between 10°C and 20°C . During this period, the WDB areas composed the area of greatest habitat use, at the expense of MCL and MCB habitats. Pallid sturgeon are generally thought to be late spring spawners, and one conclusion is that the shift to using WDB habitats over MCL and MCB habitats may represent areas used for spawning or staging by pallid sturgeon. Although no direct information is known about pallid sturgeon reproductive biology (Dryer and Sandvol 1993), interpretation of certain data indicates that pallid sturgeon are hybridizing with shovelnose sturgeon (Carlson et al. 1985; Wills et al. 2002) such that similar areas are probably being used by both species for spawning. Examination of literature concerning shovelnose sturgeon reproductive biology indicates that the species typically spawn over rock, rubble, and gravel in the main channel or on

rip-rap wing dams at water temperatures of 18–19°C (Helms 1974; Moos 1978). Shovelnose sturgeon spawning habitat seems to be distinctly different than that in the WDB areas, which consist of mostly sandy substrates. Additionally, no evidence was found during surgical implantation of the transmitters to suggest that the study specimens were sexually mature. The increased use of WDB habitats during the spring does not appear to be consistent with inferred spawning migrations.

An alternative explanation is that pallid sturgeon may have used the WDB habitats as feeding stations during the high spring flows. Snook et al. (2002) found that pallid sturgeon were often located in the Platte River just downstream of shallow sandbar habitats favorable to possible sturgeon prey items. The WDB habitats in the middle Mississippi River may function in much the same manner during high spring flows when most of the sandbar depositions in the WDB areas are underwater. The water current cuts away at the sand substrate and this may help expose benthic invertebrates common in the pallid sturgeon diet (Carlson et al. 1985), creating favorable feeding areas in WDB habitats during the spring. Additionally, the WDB areas may provide lower velocities than the MCL and MCB areas, which were more commonly used than the WDB habitat during the other seasons at lower flows. It should be noted, however, that if this is the case, radio-tagged fish were not seeking zero-current habitats, such as the WDD areas, but areas of reduced current. Other reduced-current habitats, such as the ITD (16%), were also being used to a greater extent during the spring.

With very little natural, unaltered habitat still available, it is difficult to determine critical habitat needs for pallid sturgeon. Therefore, habitat use and habitat selection by pallid sturgeon are both important pieces of information. Infrequent use does not indicate that a habitat is not important to pallid sturgeon because positive habitat selection may occur for habitats of low use. Areas of high use should therefore be viewed as areas to be protected for the benefit of pallid sturgeon commonly located there, and areas of positive habitat selection should be the type of areas considered for habitat enhancement and restoration projects.

In the middle Mississippi River, pallid sturgeon were often found in the MCL and MCB habitats. The high use of these areas by pallid sturgeon makes any negative changes to these habitats potentially harmful to pallid sturgeon. Any changes in use of these habitats or alterations to them

should be examined before future projects are undertaken. Conversely, the three of the four wing-dam habitats represent the low-use habitats examined in this study. Any alterations or changes to these habitats would have a reduced chance of harming pallid sturgeon populations due to their infrequent use of these areas.

Although the MCL is the area of highest use by middle Mississippi River pallid sturgeon, the habitat selectivity analysis presented here indicates that the ITD, MCB, and WDB areas may actually represent preferred habitats. Much like results found in other studies (Bramblett and White 2001; Snook et al. 2002), habitats may be selected by pallid sturgeon to maximize forage opportunities. These habitats should be given consideration for any future projects aimed at creating pallid sturgeon habitat because they may be necessary for the recovery of this species. Enhancement and restoration of these habitats would represent an increase in habitat diversity, which could benefit many species in addition to the endangered pallid sturgeon.

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Erratum: Habitat Use by Middle Mississippi River Pallid Sturgeon

K. L. Hurley, R. J. Sheehan, R. C. Heidinger, P. S. Wills, and B. Clevensine

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Page 1039. Pallid sturgeon with sonic tags were incorrectly described as radio-tagged.

The first sentence of the second paragraph should read as follows:

Tagged fish were found most often in the MCL habitat, followed by MCB and WDB habitats.

The first sentence of the third paragraph should read as follows:

Although the tagged sturgeon were found most often in the MCL, they exhibited stronger negative selection for MCL than for any other habitat.