North American Journal of Fisheries Management 12:744–751, 1992

Paddlefish Movements and Habitat Use in Pool 13 of the Upper Mississippi River during Abnormally Low River Stages and Discharges

CLARK T. MOEN[1] AND DENNIS L. SCARNECCHIA[2]

Department of Animal Ecology, Iowa State University
Ames, Iowa 50011, USA

JOHN S. RAMSEY[3]

U.S. Fish and Wildlife Service, Iowa Cooperative Fish and Wildlife Research Unit
Iowa State University

Abstract.—We determined the movements and habitat use by adult paddlefish *Polyodon spathula* during unusually low water levels in Pool 13 of the upper Mississippi River. Thirty-two large fish (6.3–25.4-kg) implanted with radio transmitters were located an aggregate of 812 times during March–August 1988, and spring 1989. No relation could be discovered between changes in river stage or discharge and direction of movement. No tagged paddlefish moved upstream from Pool 13, but during 1988 six fish moved downstream into Pool 14. Rates of movement were not significantly different between sexes, but the linear range for females was twice that of males. The greatest linear distance a paddlefish moved was 92 km downstream, and the greatest cumulative movement—entirely within Pool 13—was 435 km; both records were set by females. Nearly three-fourths of all contacts with paddlefish occurred in about 5% of available habitat in Pool 13. Paddlefish were located most frequently at the head of Pool 13 in the tailwaters below Lock and Dam 12. Even though the gates of Lock and Dam 12 were fully open in 1989, fish did not move upstream into Pool 12. The fish also commonly used main-channel borders with wing dams but rarely used backwaters or side channels. Water depth and velocity in areas used by paddlefish were generally within the optima suggested by current habitat suitability models, but water temperatures were usually greater than optimum.

In the last century, the paddlefish *Polyodon spathula* was extirpated in Maryland, New York, North Carolina, Pennsylvania, and Canada (Gengerke 1986), and 9 of 22 states in the species' range have reported modern declines in its abundance (Unkenholz 1986). Although excessive harvest contributed to extirpation and decline, the primary cause seems to have been human alteration of the paddlefish's large-river habitats. Knowledge of paddlefish movements and habitat requirements is essential for effective management of the species. Habitat suitability index (HSI) models and curves have been developed for the species based upon empirical data (Hubert et al. 1984) and the Delphi Technique (Crance 1987). As part of a study to identify spawning grounds of paddlefish in the upper Mississippi River (Rasmussen 1979), more than 30 large paddlefish were tagged with radio transmitters in 1988 (Moen 1989). The specific objectives of our study were to identify movement and habitat use by large paddlefish (most of which were gravid females) during low water to compare our results with those of a previous study of smaller fish in the same river reach under normal water conditions (Southall 1982), and to examine the validity of existing HSI curves for paddlefish (Hubert et al. 1984; Crance 1987). Inasmuch as the habitat requirements of paddlefish may change with fish size (Coker 1930; Thompson 1933) and with varying water conditions between years (Southall 1982), we expected information from this study to supplement and clarify the existing information on paddlefish habitat use.

Study Site

The study was conducted in Pool 13 of the upper Mississippi River. Pool 13 extends from Lock and Dam 12 at Bellevue, Iowa, 55 km downstream to Lock and Dam 13 at Clinton, Iowa (Figure 1). Pools along the upper river were created by locks

[1] Present address: South Dakota Department of Game, Fish and Parks, Blue Dog State Fish Hatchery, Rural Route 1, Box 22A, Waubay, South Dakota 57273, USA.

[2] Present address: Department of Fish and Wildlife Resources, College of Forestry, Wildlife and Range Sciences, University of Idaho, Moscow, Idaho 83843, USA.

[3] Present address: U.S. Fish and Wildlife Service, Office of Information Transfer, 1201 Oak Ridge Drive, Suite 200, Fort Collins, Colorado 80525-5589, USA.

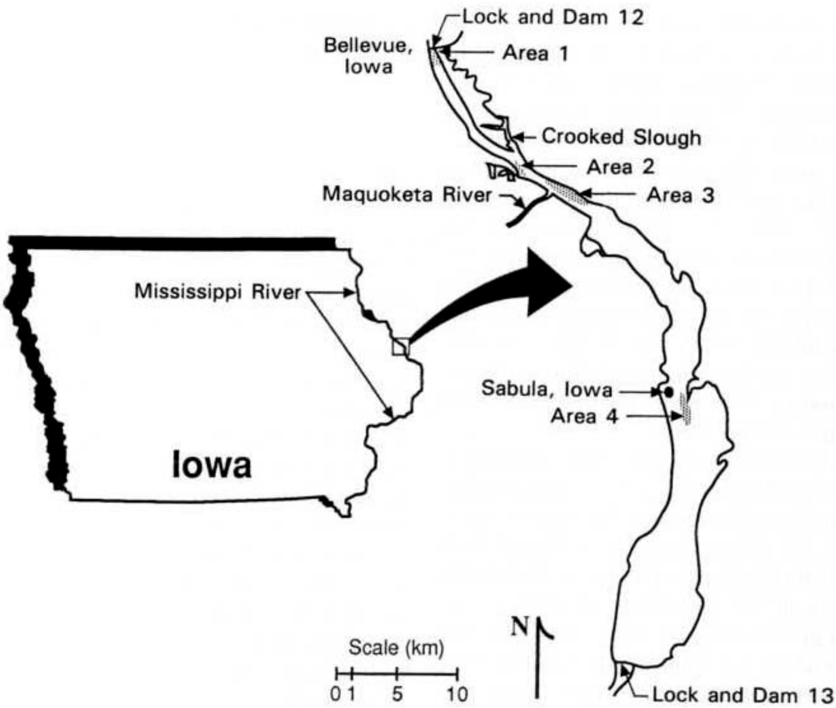

FIGURE 1.—Study area, Pool 13, upper Mississippi River.

and dams constructed for navigation by the U.S. Army Corps of Engineers.

The Fish Technical Section of the Upper Mississippi River Conservation Committee identified seven general habitat types in the upper river (Rasmussen 1979): tailwaters, main channels, main-channel borders, side channels, sloughs, lakes, and ponds. We subdivided the main-channel borders into areas with or without wing dams and combined sloughs, lakes, and ponds into one category: backwaters.

Precipitation and river discharges in the midwestern USA were anomalously low for two consecutive years, 1987 and 1988. During March–August 1988, mean monthly precipitation at Lock and Dam 11 at Dubuque, Iowa, averaged 42% below the previous 125-year monthly means. For this period, the mean monthly flows through Lock and Dam 13 at Clinton, Iowa, also averaged 42% lower than the previous 47-year monthly means. The gates of Locks and Dams 12 and 13 were therefore never fully opened in 1988. From 31 March to 10 April 1989, however, the gates of Lock and Dam 12 were fully opened, allowing the river to flow freely and providing fish access to Pool 12.

In our study, data on river conditions in 1988 were separated into two distinct periods according to rate of discharge. During spring (11 March–20 May), average daily discharge was 1,530 m^3/s and average tailwater stage was 2.17 m at Lock and Dam 12. Surface water temperature in the main channel was 13.8°C on 2 May and rose steadily to 19.2°C by mid-May (average, 17.1°C). During summer (21 May–12 August), discharge and tailwater stage averaged 496 m^3/s and 1.05 m, respectively, and were significantly lower ($P < 0.01$) and more stable than during spring. Water temperature increased during the summer from 19.7 to 27.4°C (average, 24.9°C)

Methods

Radio equipment was obtained from Advanced Telemetry Systems, Isanti, Minnesota. Transmitters were manufactured to activate once every 2 s for up to 2.5 years and had frequencies between 48.021 and 48.429 MHz. A transmitter and the attached 60-cm wire whip antenna weighed 134 g in air (0.5–2.1% of fish weight). Radio receivers automatically scanned through the programmed series of radio frequencies during tracking. A large four-element Yagi antenna mounted in a boat completed the radio telemetry system.

Thirty-five paddlefish were collected from the tailwaters of Lock and Dam 12 in 1988: 29 by snagging between 11 and 17 March and 6 by netting during summer. Details of the capture methods were provided by Moen (1989). Radio transmitters were surgically implanted by established techniques (Hart and Summerfelt 1975; Southall 1982; Brantly 1987). The 35 paddlefish in this study averaged 97 cm in body length (range, 75–114 cm) and 15.7 kg in weight (range, 6.3–25.4 kg), almost twice the average weight of the fish studied by Southall (1982). The 35 fish were classified into four groups: males (mature and immature), immature females, maturing females, and mature females (Moen 1989).

From 25 March to 12 August 1988, searches to locate radio-tagged paddlefish were conducted daily by boat during daylight hours. An airplane overflight of Pools 12–16 was made on 11 August 1988 to find five fish that had not been located in the study area during the previous 4–6 weeks. Two fish were contacted during the flight and were again located by boat on 12 August. Movements were also monitored in March–April 1989 while the gates of Lock and Dam 12 were fully opened.

The location of each fish was plotted on U.S. Army Corps of Engineers maps (U.S. Army Corps of Engineers 1982) after visual triangulation of prominent terrestrial landmarks and identification of the fish's proximity to in-river structures such as wing dams, islands, or slough entrances. A fish was considered to be associated with a structure (e.g., a wing dam) when a contact was within 200 m of the structure. Date, time, and habitat type (Rasmussen 1979) were recorded at each contact. Between 11 March and 12 August 1988, the 32 fish that provided usable data were collectively located 774 times. Contacts with individual fish ranged from 5 to 39 (mean, 24; median, 26). At 57 randomly selected sites where fish were located, six habitat variables were measured: surface water temperature (°C), water depth, substrate type, and water velocity at three depths (30 cm below surface, 0.6 of depth, and 30 cm above the substrate). Data on fish movements and habitat use were analyzed with the Statistical Analysis System (SAS; Helwig and Council 1979). In all analyses, a P-value of less than 0.05 was necessary to reject a null hypothesis. Habitat use and preference of paddlefish were evaluated with the aid of Ivlev's electivity index: $E = (r_i - p_i)/(r_i + p_i)$; r_i is the proportional usage of habitat i, and p_i is the proportional abundance of habitat i (Ivlev 1961; Southall 1982). The habitat characteristics of the 57 sites were compared with HSI curves of Hubert et al. (1984) and Crance (1987).

Results

Movement

The movements of paddlefish varied greatly among fish and concurrent group movement was not apparent. Of the 27 fish that were located more than nine times each, only 5 exhibited directional movements that significantly differed from random as determined with a nonparametric runs up-and-down test (Gibbons 1976). Each of these five fish made a series of downstream movements, and four moved downstream into Pool 14 (three in June or July and one in October). In 1988, six tagged fish moved downstream through Lock and Dam 13 into Pool 14 but no fish moved upstream through either Lock and Dam 12 or 13 during the study. The greatest directional movement was 92 km by a maturing female between May and August 1988. The greatest cumulative movement was 435 km by a mature female entirely within Pool 13; much of this movement occurred during summer low-water conditions. Even when the gates of Lock and Dam 12 were fully opened for 10 consecutive days in April 1989, no tagged paddlefish moved from Pool 13 into Pool 12.

Whether or not paddlefish moved upstream when discharge and stage increased could not be determined. Correlation analysis indicated no relationship between discharge or tailwater stage at Lock and Dam 12 and mean direction of fish movement for any of the fish categories defined.

Females seemed to move greater distances than males. Analysis of variance indicated the linear range (the distance between the lowermost and uppermost telemetry contacts with a fish in the river) was significantly less for males (mean, 19 km; range, 13–25) than for females (mean, 39 km; range, 14–60). This analysis was only performed for the 15 fish with the largest number of contacts (range, 27 to 37 contacts; mean, 33; SD, 3.3). However, mean movement rates, calculated for periods of less than 48 h, were not significantly different between spring (mean, 0.086 km/h) and summer (mean, 0.097 km/h), nor between males (mean, 0.077 km/h) and females (mean, 0.092 km/h).

Habitat Use

Of the 774 contacts in 1988, 304 encounters (39%) were in tailwaters, 260 (34%) in main-channel borders with wing dams, and 128 (16%) in

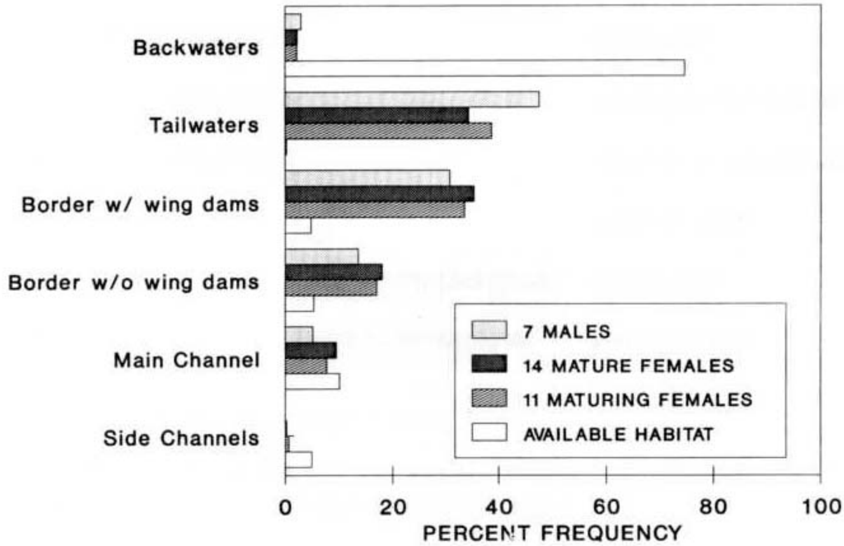

FIGURE 2.—Use of habitat types by paddlefish during spring and summer (11 March–12 August) 1988 in Pool 13, upper Mississippi River (w/ = "with"; w/o = "without").

main-channel borders without wing dams (Figure 2; Table 1). Few contacts with radio-tagged paddlefish were in the main channel (8%), backwaters (2%), or side channels (< 1%). Three-fourths of all contacts were in about 5% of available habitat, and only 2% of the contacts were in the most abundant habitat type, the backwaters.

The distribution of contacts among the habitat types did not differ substantially between spring (583 encounters) and summer (191 encounters). During both seasons, paddlefish were most commonly located in the tailwaters (37% during spring, 48% during summer). Contacts in main-channel borders with wing dams were 34% of all contacts in spring and 33% in summer. Number of contacts in main-channel borders without wing dams decreased from 20% in spring to 7% in summer. Use of backwaters remained low in both seasons (≤ 5%). Ten fish were located collectively a total of only 14 times in the most lacustrine backwater area immediately above Lock and Dam 13. Use of the main channel (< 10%) and side channels (1%) remained low in both seasons.

During spring, frequency of use of the tailwaters and main-channel borders with and without wing dams differed only slightly among males, mature females, and maturing females. During summer, paddlefish were contacted frequently in the tail-

TABLE 1.—Numbers of contacts with paddlefish in each habitat type during spring and summer 1988 in Pool 13 of the upper Mississippi River. Numbers in parentheses are column percentages; N is the number of radio-tagged fish in each fish category.

Habitat type	Males		Mature females		Maturing females		All	
	Spring (N = 6)	Summer (N = 6)	Spring (N = 11)	Summer (N = 11)	Spring (N = 11)	Summer (N = 9)	Spring (N = 28)	Summer (N = 26)
Tailwaters	58 (40)	36 (65)	72 (32)	33 (41)	83 (38)	22 (40)	213 (36)	91 (48)
Main-channel border with wing dams	47 (33)	14 (26)	76 (34)	32 (40)	74 (34)	17 (31)	197 (34)	63 (33)
Main-channel border without wing dams	24 (17)	3 (5)	51 (23)	4 (5)	40 (19)	6 (11)	115 (20)	13 (7)
Main channel	8 (6)	2 (4)	22 (10)	7 (8)	17 (8)	4 (7)	47 (8)	13 (7)
Backwaters	6 (4)	0	2 (1)	5 (6)	1 (<1)	5 (9)	9 (2)	10 (5)
Side channels	0	0	1 (<1)	0	1 (<1)	1 (2)	2 (<1)	1 (<1)
All	143	55	224	81	216	55	583	191

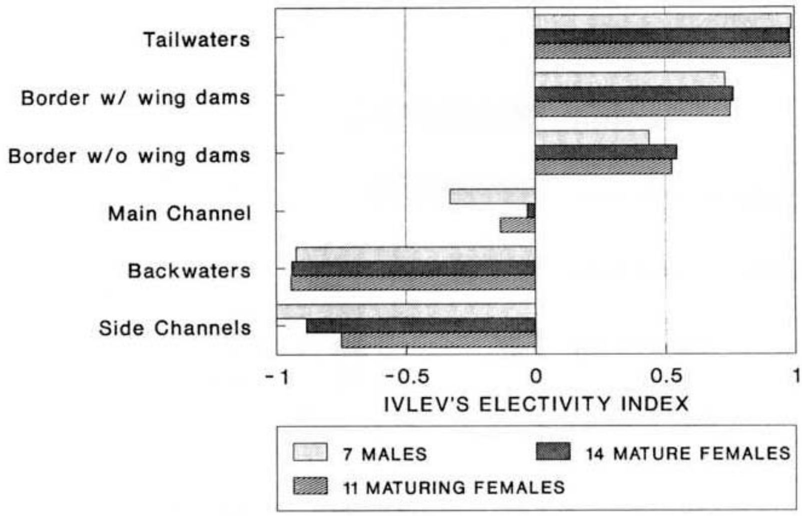

FIGURE 3.—Ivlev's electivity index values for habitat preference by paddlefish during spring and summer (11 May–12 August) 1988 in Pool 13, upper Mississippi River (w/ = "with"; w/o = "without").

waters, males more so than females. Sixty-five percent of the contacts with males and about 40% of the contacts with mature and maturing females were in tailwaters (Table 1). As in spring, the next most numerous contacts were in main-channel borders with wing dams, and use of the main channel was low (< 10% for males, mature females, and maturing females). Only 2% of the contacts with maturing females and none with males or mature females were in side channels. No males were contacted in backwaters during summer, and less than 10% of the contacts with mature and maturing females were in backwaters.

These results indicate that paddlefish used habitats selectively in the river. Only two habitats were used in proportion to availability: the main channel by mature females during spring, and main-channel borders without wing dams by mature females during summer. Ivlev's electivity index indicated that for all fish and seasons combined, paddlefish strongly selected tailwaters (E = 0.99) and main-channel borders with wing dams (E = 0.74; Figure 3). Males, mature females, and maturing females displayed similar selection for these two habitats during spring and summer.

The main channel was avoided weakly by females ($-0.16 \leq E \leq 0$) and more so by males (summer E, −0.47). The greater use of the main channel by females than by males probably was related to the greater distances moved by females. During both seasons, paddlefish avoided backwaters (average E, −0.91) and side channels (average E, −0.85).

In 1988, 69% of the contacts with paddlefish were in four short areas in Pool 13 (Figure 1). Forty-six percent were in area 1, which was the uppermost kilometer of the pool and included the tailwaters. When paddlefish were not located within the tailwaters, they were frequently near one of the three wing dams in area 1. Six percent of the contacts were in area 2, approximately 2 km long and 9.6 km downstream from Lock and Dam 12. This area included the four wing dams across from the entrance to Crooked Slough. Eleven percent of the contacts were in area 3, 3 km long and 2 km downstream from area 2. This area featured a series of nine wing dams opposite the mouth of the Maquoketa River. Six percent of all contacts were in area 4, 2 km long and 19.2 km below area 3. Area 4, across from Sabula, Iowa, had three wing dams. Only 13% of all contacts were in the 8-km reach between areas 1 and 2, 4% were in the 2-km reach between areas 2 and 3, 10% were in the 19-km reach between areas 3 and 4, and 3% were in the 18-km reach below area 4.

Comparison with HSI Curves

Paddlefish were usually contacted at sites with depths and velocities within acceptable or optimal ranges (HSI values of 0.5–1.0; Hubert et al. 1984; Crance 1987). Ninety-one percent of the locations were deeper than 3 m, as is the optimal depth range according to Hubert et al. (1984). However, 67% of the locations were deeper than 5 m, the greatest depth on the HSI curve produced by Hubert et al. (1984), and 30% of these locations were deeper than 7 m, the limit of the optimal range according to Crance (1987). Eighteen percent of the locations in 1988 had mean current velocities less than 0.07 m/s, within the optimal range, and 95% had velocities less than 0.30 m/s, within the acceptable range of the HSI models generated by Hubert et al. (1984) and Crance (1987). Mean current velocity at locations where we contacted paddlefish was 0.16 m/s (SD, 0.09; range, 0.01–0.50).

Water temperatures where we located paddlefish were usually higher than HSI optima. Only 4% of the contacts were made where temperatures were within the optimal range of 7–20°C (Hubert et al. 1984); 37% of the contacts were made where temperatures were in the optimal range of 13–24°C reported by Crance (1987).

Discussion

Movement

Results of our study suggested that interpool movements of paddlefish may be impeded by closed lock gates and by the absence of fish passage structures at locks and dams, although paddlefish did not move upstream through Lock and Dam 12 when the gates were opened for 11 d in spring 1989. Several paddlefish were located immediately below Lock and Dam 12 at any time during the study. One fish in particular exhibited repeated upstream and downstream movements between Lock and Dams 12 and 13. Dams have been reported to prevent upstream movements of paddlefish in the upper Mississippi River (Coker 1929; Southall and Hubert 1984), the Missouri River (Rehwinkel 1978; Rosen et al. 1982), and the Osage River (Russell et al. 1980). Furthermore, the longest documented paddlefish movements have occurred in open, undammed river systems or stretches (Russell 1986).

Paddlefish can pass downstream through partially closed dam gates without sustaining major injuries (Coker 1929; Southall 1982). Although Gengerke (1978) suggested that paddlefish may use the locks to move between pools of the upper Mississippi River, no radio-tagged paddlefish in our study were contacted directly below, above, or inside a navigation lock.

Direction of paddlefish movement was not related to changes in either flow through Lock and Dam 12 or tailwater stage for any group (males, maturing females, mature females, all females, and all fish) during either spring or summer. This result contrasts markedly with results from several other studies. Purkett (1963) and Pasch et al. (1978, 1980) reported that paddlefish moved upstream with increasing water level or discharge, especially during spring. Those studies revealed a relationship between marked increases in recreational or commercial harvests of paddlefish in tailwater areas and substantial rises in river levels. In our study, some individuals exhibited the expected upstream movement. However, other individuals moved downstream under the same conditions and obscured the relationship between rising water levels and upstream movements. Perhaps the modest spring flood and low waters of 1988 were insufficient to induce major, synchronized upstream movements. Graham et al. (1975) and Southall (1982) also had difficulty in determining a relationship between river conditions and direction of movement for all periods of changing river stage.

Habitat Use

Habitat use by the large paddlefish in 1988 showed both similarities with and differences from habitat use by Southall's (1982) smaller fish. Paddlefish in both studies were most frequently located in the tailwaters and main-channel borders with wing dams during spring and summer. Four of every 10 contacts with radio-tagged paddlefish in 1988 were made in the tailwaters below Lock and Dam 12, a frequency twice that found by Southall (1982) in 1980 and 1981. During low river levels, the scour holes and eddies in tailwater areas seemed to be more important to large paddlefish than to small ones.

Similar to Southall's (1982) findings, about half of all contacts in 1988 were made in main-channel borders. Paddlefish were contacted twice as often in main-channel borders with wing dams than in main-channel borders without wing dams. Our results indicate that the protection from current offered and the eddies and scour holes created by wing dams (or similar natural structures such as sand bars; Rosen et al. 1982) are favorable for paddlefish. Southall (1982) drew a similar conclusion.

Overall, more than two-thirds of all contacts with radio-tagged paddlefish were made in four rather restricted areas of Pool 13. These areas, which were less than 10% of the area of the pool, had several characteristics that may have attracted paddlefish. Each area, including the heavily used tailwaters below Lock and Dam 12, had a series of at least three wing dams. Furthermore, each contained deep water. A scour hole more than 6 m deep had formed behind at least one of the wing dams in each area, and the average depth in the tailwaters was 15.7 m. During spring, when the gates were closed, paddlefish may have been searching these wing dam or tailwater habitats for possible spawning sites. These habitats often have rocky substrates and currents favorable for paddlefish reproduction (Purkett 1961). Also, these habitats generally were immediately downriver from backwaters, which may be important food-producing areas for paddlefish (Alexander 1915; Rosen et al. 1982; Eckblad et al. 1984; Southall and Hubert 1984).

The turbulent currents in the tailwaters and perhaps in deep scour holes may allow paddlefish to swim slowly yet remain almost stationary while feeding on drifting invertebrates. The depths of these areas may offer some form of protection or cover that is difficult to define without further study. Other seemingly similar areas in Pool 13 had neither deep scour holes nor slow and variable currents and were not near an entrance to a backwater. Paddlefish used these areas only occasionally.

Unlike Southall's (1982) fish, paddlefish in our study occasionally used the lacustrine habitat above Lock and Dam 13 in 1988. The reasons for this difference could not be determined. Conversely, we only contacted five fish (about 1% of all contacts) in the backwaters of Crooked Slough during spring and summer 1988, whereas Southall (1982) made about 15% (80 of 518) of his contacts in these backwaters. Reasons for the more infrequent use of the Crooked Slough backwater in 1988 than in 1980 and 1981 are also unclear. Perhaps the low water levels during 1987 and 1988 rendered some backwaters either too shallow, too vegetated, or too warm for paddlefish during summer. Observations in Crooked Slough in 1988 and 1989 indicated that some areas were less than 1 m deep during summer; this depth is considered unsuitable for paddlefish (Crance 1987). Excessive growth of filamentous algae in these shallow areas may also decrease habitat suitability. Southall (1982) observed that paddlefish moved out of Crooked Slough when water temperature approached 30°C in 1980, and although we did not measure water temperatures in Crooked Slough in 1988, high water temperatures are common during droughts. Sheaffer (1984) found water temperatures to be significantly higher in backwaters than in the main channel ($P < 0.10$).

Comparison with HSI Curves

The habitat characteristics at sites where paddlefish were contacted were generally consistent with the two HSI models published for adult paddlefish (Hubert et al. 1984; Crance 1987). Large paddlefish of Pool 13 evidently used areas with greater depths than the models indicated (Hubert et al. 1984; Crance 1987). We do not know whether the fish in deep areas were on the bottom or swimming above it. Our observations of the snag fishery provided circumstantial evidence that many adult paddlefish are near the bottom throughout the winter. Some of the best paddlefish snagging in the upper Mississippi River occurs below Lock and Dam 12 (Anderson and Ackerman 1977; Carlson and Bonislawsky 1981), where a particularly deep (about 24 m) scour hole occurs (Tom Boland, Iowa Department of Natural Resources, personal communication). Deep water may provide valuable year-round habitat for paddlefish.

The high water temperatures at paddlefish locations may have been a result of the low flows of 1988. Although we did not measure water temperature routinely where we contacted paddlefish, we did measure temperatures near 30°C in the main channel and in backwater areas during summer. Paddlefish perhaps used the coolest available water during the warm, dry weather and drought conditions of 1988.

Specific habitat use by paddlefish in a given year may be a response to not only general habitat characteristics in the upper Mississippi River but also to specific constraints and conditions. Results from our study, which differed from those of Southall (1982) in the same river reach, underscore the need to evaluate habitat use under different hydrological and ecological conditions.

Acknowledgments

This is journal paper J-14041 of the Iowa Agriculture and Home Economics Experiment Station, Ames, project 2815. Cooperators with the Iowa Cooperative Fish and Wildlife Research Unit are the Iowa Department of Natural Resources, the U.S. Fish and Wildlife Service, and Iowa State University. The Iowa Department of Natural Resources provided financial support for this study. We thank John Pitlo, Maurice Anderson, Dennis Weiss, and Gary Curtis for their valuable inputs and assistance. Helpful reviews of the manuscript were also provided by C. M. Alexander, K. Graham, and D. Unkenholz.

References

Alexander, M. L. 1915. More about paddlefish. Transactions of the American Fisheries Society 45:34–39.

Anderson, M., and G. L. Ackerman. 1977. Fire in the hole. Iowa Conservationist 36(2):8–9.

Brantly, T. B. 1987. Paddlefish movements in the upper Alabama River. Master's thesis. Auburn University, Auburn, Alabama.

Carlson, D. M., and P. S. Bonislawsky. 1981. The paddlefish (*Polyodon spathula*) fisheries of the midwestern United States. Fisheries (Bethesda) 6(2):17–27.

Coker, R. E. 1929. Keokuk Dam and the fisheries of the upper Mississippi River. U.S. Bureau of Fisheries Bulletin 45:87–139.

Coker, R. E. 1930. Studies of common fishes of the Mississippi River at Keokuk. U.S. Bureau of Fisheries Bulletin 45:141–225.

Crance, J. H. 1987. Habitat suitability index curves for paddlefish, developed by the Delphi technique. North American Journal of Fisheries Management 7:123–130.

Dillard, J. G., L. K. Graham, and T. R. Russell, editors. 1986. The paddlefish: status, management and propagation. American Fisheries Society, North Central Division, Special Publication 7, Bethesda, Maryland.

Eckblad, J. W., C. S. Volden, and L. S. Weilgart. 1984. Allochthonous drift from backwaters to the main channel of the Mississippi River. American Midland Naturalist 111:16–22.

Gengerke, T. W. 1978. Paddlefish investigations. Iowa Conservation Commission, U.S. National Marine Fisheries Service, Project 2-225-R, Segment 1-3, Final Report, Des Moines.

Gengerke, T. W. 1986. Distribution and abundance of paddlefish in the United States. Pages 22–35 *in* Dillard et al. (1986).

Gibbons, J. D. 1976. Nonparametric methods for quantitative analysis. Holt, Rinehart and Winston, New York.

Graham, L. K., T. R. Russell, and E. J. Hamilton. 1975. Maintenance of the Osage River paddlefish fishery. Missouri Department of Conservation Quarterly Report to the U.S. Army, Corps of Engineers, Kansas City, Missouri.

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

Helwig, J. T., and K. A. Council. 1979. SAS user's guide. SAS Institute, Cary, North Carolina.

Hubert, W. A., S. H. Anderson, P. D. Southall, and J. H. Crance. 1984. Habitat suitability index models and instream flow suitability curves: paddlefish. U.S. Fish and Wildlife Service Biological Services Program FWS/OBS 82(10.80).

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut.

Moen, C. T. 1989. Paddlefish movements and habitat use in Pool 13 of the upper Mississippi River during low water conditions. Master's thesis. Iowa State University, Ames.

Pasch, R. W., P. A. Hackney, and J. A. Holbrook. 1978. Ecology of the paddlefish, *Polyodon spathula* (Walbaum), in Old Hickory Reservoir, Tennessee, with emphasis on first year life history and the effects of impingement at Gallatin Steam Plant on the population. Tennessee Valley Authority, Division of Water Resources, Development Report, Knoxville, Tennessee.

Pasch, R. W., P. A. Hackney, and J. A. Holbrook II. 1980. Ecology of paddlefish in Old Hickory Reservoir, Tennessee, with emphasis on first-year life history. Transactions of the American Fisheries Society 109:157–167.

Purkett, C. A., Jr. 1961. Reproduction and early development of the paddlefish. Transactions of the American Fisheries Society 90:125–129.

Purkett, C. A., Jr. 1963. The paddlefish fishery of the Osage River and the Lake of the Ozarks, Missouri. Transactions of the American Fisheries Society 92: 239–244.

Rasmussen, J. L. 1979. A compendium of fishery information on the upper Mississippi River. Upper Mississippi River Conservation Commission, Rock Island, Illinois.

Rehwinkel, B. J. 1978. The fishery for paddlefish at Intake, Montana, during 1973 and 1974. Transactions of the American Fisheries Society 107:263–268.

Rosen, R. A., D. C. Hales, and D. G. Unkenholz. 1982. Biology and exploitation of paddlefish in the Missouri River below Gavins Point Dam. Transactions of the American Fisheries Society 111:216–222.

Russell, T. R. 1986. Biology and life history of the paddlefish—a review. Pages 2–20 *in* Dillard et al. (1986).

Russell, T. R., L. K. Graham, D. M. Carlson, and E. J. Hamilton. 1980. Maintenance of the Osage River–Lake of the Ozarks paddlefish fishery. Missouri Department of Conservation, Final Report, Columbia.

Sheaffer, W. A. 1984. Importance of backwater area confluences to the fishes and macroinvertebrates of the upper Mississippi River, Pool 13. Master's thesis. Iowa State University, Ames.

Southall, P. D. 1982. Paddlefish movement and habitat use in the upper Mississippi River. Master's thesis. Iowa State University, Ames.

Southall, P. D., and W. A. Hubert. 1984. Habitat use by adult paddlefish in the upper Mississippi River. Transactions of the American Fisheries Society 113: 125–131.

Thompson, D. H. 1933. The finding of very young *Polyodon*. Copeia 1933:31–33.

Unkenholz, D. G. 1986. Effects of dams and other habitat alterations on paddlefish sport fisheries. Pages 54–61 *in* Dillard et al. (1986).

U.S. Army Corps of Engineers. 1982. Upper Mississippi River navigation charts. U.S. Army, Corps of Engineers, North Central Division, Chicago, Illinois.