Minnesota Department of Natural Resources
Investigational Report 449, 1996

SEASONAL HABITAT USE AND MOVEMENTS OF MUSKELLUNGE IN THE MISSISSIPPI RIVER[1]

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Abstract--Radio telemetry was used to determine seasonal movement and habitat use, and identify spawning areas for muskellunge *Esox masquinongy* in the Mississippi River. The study area consisted of three distinct river sections with boundaries defined by four dams. Characteristics unique to riverine systems best describes Section 1, while most features in Section 3 and all of Section 2 are characteristic of reservoir habitats. Thirteen muskellunge, of which only one was located in Section 2, were implanted with radio transmitters and tracked by boat (open-water) and aircraft (ice cover). Seasonal changes in movement and habitat use were strongly influenced by river section characteristics. Total range length was greater in Section 3 (34.0 km mean) than in Section 1 (14.2 km mean). Distances between wintering areas and spawning sites were four times greater in Section 3 than Section 1. All muskellunge in Section 3 moved upstream to spawn and downstream to overwinter, while no directional pattern was evident in Section 1. All tagged muskellunge established both a winter and summer range with winter ranges distinctly separate from summer ranges only in Section 3. Winter ranges were longer in Section 3 (5.9 km mean) than in Section 1 (1.3 km mean). Coinciding with a period of limited movement, overwintering occurred in pools (Section 1) and the main channel (Sections 2 and 3), and varied in depth from 2.5 to 4.1 m. During summer, activity patterns were affected the least by differences in river characteristics, when movements and ranges were similar between Sections 1 and 3. Shallow water habitats averaging 1.6 m in depth were most frequently used in both Sections 1 and 3 during the summer. Seven spawning sites that contained 19 spawning areas were identified in the three study sections. Except Section 2, all spawning areas were located in backwater habitats characteristic of riverine stretches of the Mississippi River. Spawning was documented at water temperatures averaging 10.9 °C, in depths averaging 81 cm, and over substrates consisting of muck, silt, sand, and decomposing vegetation.

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[1] This project was funded in part by the Federal Aid in Sport Fish Restoration (Dingel-Johnson). Completion Report, Study 622, D-J Project F-26-R Minnesota.

Introduction

The threat of increased damage to prime muskellunge habitats was one of four factors cited as affecting the future of muskellunge (Crossman 1986). Dombeck (1986) and Hanson et al. (1986) viewed habitat protection as the most critical program for long term maintenance of muskellunge populations. Recognition of the importance of habitat is best illustrated by examining behavioral responses as they relate to environmental and physical factors. Muskellunge habitat requirements change with their size and monitoring this relationship is essential in analyzing critical habitat needs for all life stages.

Gerking (1959) suggested applying results from behavioral studies to specific problems influencing fish populations. The advancement of biotelemetry techniques has greatly enhanced the quantity and quality of behavioral information generated from field studies. Past use of biotelemetry techniques in monitoring muskellunge behavior in lacustrine systems has provided detailed knowledge of their summer, winter and spawning habitat use and seasonal activity patterns (Miller and Menzel 1986a; 1986b; Strand 1986; Dombeck 1979; Minor and Crossman 1978; and Crossman 1977). In lotic systems, however, information detailing habitat use and movement has been inferred from standard survey and mark and recapture studies (Monaghan 1985; Osterberg 1985; Axon and Kornman 1986; Brewer 1980; Harrison and Hadley 1978; Miles 1978; Parsons 1959).

Approximately 1% of the total freshwater area of North America contains muskellunge (Carlander et al. 1978). For Minnesota waters, this includes 81 lakes (193,900 ha) and 3 major river systems representing the largest freshwater acreage in the United States. A significant number of these waters contain native self-sustaining muskellunge populations which deserve special attention. This is especially important for lotic systems where critical habitats are vulnerable to flow manipulations.

The Mississippi River is the largest riverine system supporting a native muskellunge population in Minnesota. Successful natural reproduction occurs in the Mississippi River, although past management did include periodic stocking. Presently, the dynamics of the Mississippi River muskellunge population are unknown. The purpose of this study was to determine seasonal movements, habitat use, and identify specific muskellunge spawning areas in the Mississippi River. The addition of this type information will provide the basis for future evaluations on the status of Mississippi River muskellunge.

Study Area

The study area comprises 118 km of the Mississippi River located in central Minnesota (Figure 1). Four dams divide the study area into three distinct study sections. The dams function as hydropower sources for wood and hydropower industries, and serve as effective barriers to upstream fish migration. The primary fish species found in the study area are muskellunge, walleye *Stizostedion vitreum*, northern pike *Esox lucius*, smallmouth bass *Micropterus dolomieu*, white sucker *Catostomus commersoni*, redhorse *Moxostoma spp.*, and common carp *Cyprinus carpio*. Recreational access is ample, with both private and public access sites located throughout the study area.

Study Section 1, between Little Falls and Brainerd, is the longest (64 km) and the most riverine of the three sections. Approximately 90% of Section 1 features a series of well defined run-pool sequences interspersed with a few rapids. A maximum depth of 4.8 m occurs in riverine pools scattered throughout the upper and middle stretches of this section. A short stretch with reservoir characteristics is present above the Little Falls Dam, where maximum depth is 8.2 m. Most of the river corridor in Section 1 is bordered by steep banks and deciduous forests. Urban development is primarily concentrated near the dam sites, but expansion into undeveloped tracts is occurring at both upstream and downstream dams. Study Section 2 stretches from Little Falls Dam to Blanchard Dam, a distance of 15 km. The 39 km stretch bounded by Blanchard and Sartell Dams defined Section 3. All of Section 2 and

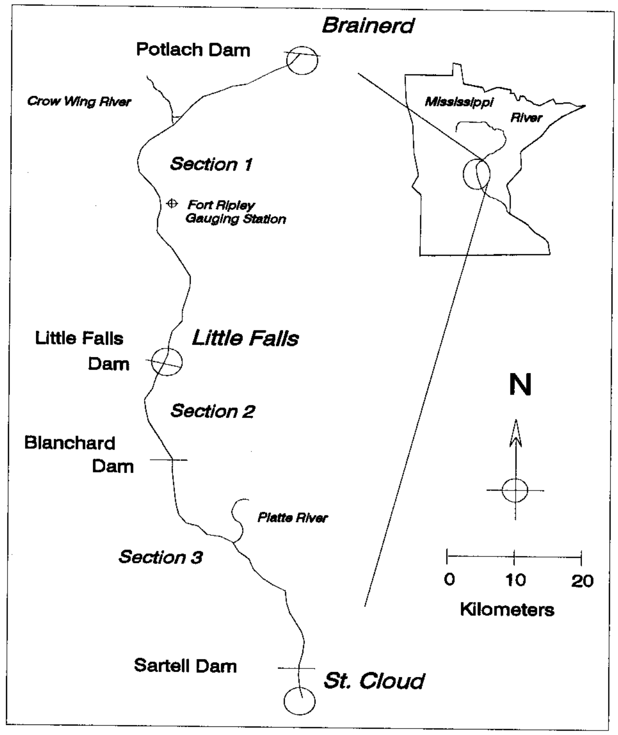

Figure 1. Mississippi River muskellunge telemetry project study area, Brainerd Dam to Sartell Dam, 1990 to 1993. Study area was divided into three sections between the four dams.

approximately 60% of Section 3 have features characteristic of reservoirs. Riverine characteristics are present in Section 3, occurring downstream from Blanchard Dam to approximately the confluence of the Platte River. Both reservoir sections feature a continuous main channel that ranges in depth from 2.1 to 13.7 m. Sections 2 and 3 have more urban and agricultural development along the river corridor. One major river (Crow Wing) and numerous smaller tributaries drain into the study area.

Discharges are manipulated seasonally to accommodate water users downstream and to prepare for annual spring runoff. For the Mississippi River, April peak flows are typically followed by a precipitous decline in summer, and stable flows during fall and winter (Figure 2). Although partly regulated by dams within the study area, flow is primarily regulated by a series of headwater dams and reservoirs located in north central Minnesota.

Methods

Thirteen muskellunge were captured (11 by night electrofishing and 2 by angling) and implanted with radio tags during 1990 and 1991; 8 muskellunge in Section 1, 1 in Section 2, and 4 in Section 3. Study fish averaged 1,024 mm TL (range 920 - 1,210 mm) and 8.1 kg (range 6.1 - 13.8 kg). All study fish were mature. Although efforts were expended to ensure equal representation from both sexes, only four of the tagged muskellunge were males.

Fish were anesthetized immediately after capture, placed in a surgical tube, and transmitters surgically implanted into the body cavity following the techniques described by Strand (1986) and Ross and Kleiner (1982). Radio transmitters were 61.9 mm long, 28.6 mm in diameter, weighed 73 g, and were powered by a lithium battery. Each transmitter operated at a unique output frequency within the 48 to 49 MHz band and separated by a minimum of 20

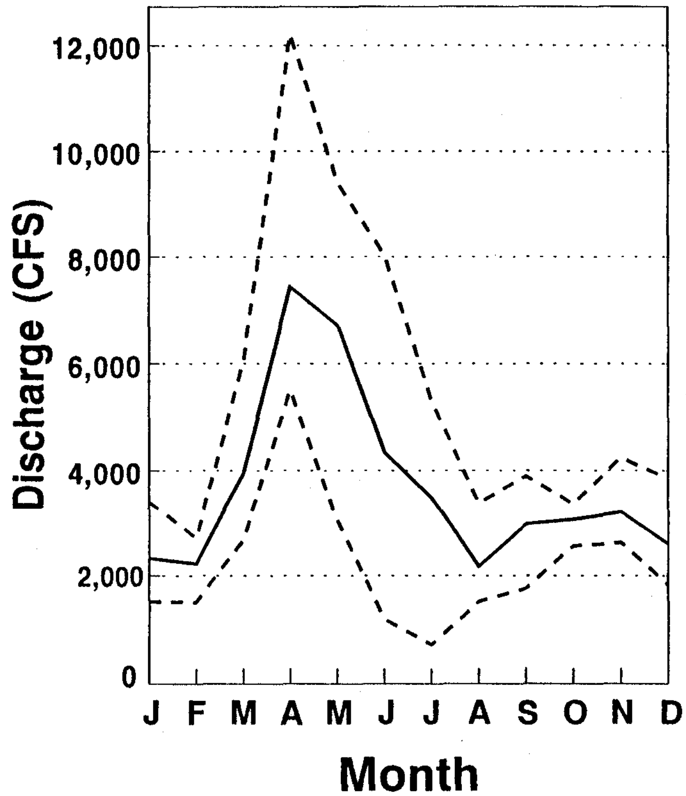

Figure 2. Discharge at the Fort Ripley gauging station (Section 1) in the Mississippi River, 1987-1993. Solid line represents mean discharge and dashed lines represent minimum and maximum discharges.

Khz. Each fish was also marked with a numbered floy spaghetti tag placed anterior to the dorsal fin (White and Beamish 1972). Post-operative fishes were treated with an antiseptic and placed in an oxygenated recovery tank. All muskellunge were released at their capture site within approximately 30 minutes, except for angled fish which were transported to and released at the surgical site.

Monitoring began the first day after a tagged fish was released and continued through June 1993, or loss of the study fish. Fish were located a minimum of 1-2 times weekly by boat during the open water period in Sections 2 and 3. In Section 1, fish were frequently monitored up to four times a week during open water periods. Aerial tracking was conducted once a week during periods of ice cover, weather permitting. Radio tracking was conducted primarily during daylight hours, except during spring when effort was increased in Section 1 to include night monitoring of tagged fish and spawning areas.

Radio telemetry equipment consisted of a programmable scanning receiver, hand-held loop antenna, and omnidirectional whip antennae of various lengths. The hand-held loop antenna was used to search for transmitter signals and provide general locations. When in proximity to radio tagged fish, an electric trolling motor or push-pole was used to maneuver over a radio tagged fish. A progression of decreasing lengths of whip antennae (30, 15, and 6 cm) was employed to define exact locations. Maximum signal strength with the shortest whip antenna identified the actual location of the fish within approximately 1 m. Visual observations of tagged muskellunge were possible in clear water, and used to verify exact fish locations.

Loran position and triangulation with river features and visual landmarks were used to plot fish locations on contour maps. At each fish location the following information was recorded: date, contact time, water depth, water temperature, substrate, cover, habitat type, longitude, and latitude. During open water periods, water depth was determined by direct measurement or with a depth sounder. For periods of ice cover, water depths were obtained from contour maps. Substrate and cover type was determined during the open water period only in Section 1. Substrate was identified by visual observation or probing with a push-pole, and categorized as sand, silt, gravel, cobble, boulder, or a composite of substrate types. Cover was categorized as open water (no obvious cover), vegetation, timber, rocks (large cobble to boulder), deep water, and bottom morphology. General habitat type based on characteristics common to riverine and reservoir habitats included: pool (riverine deep water), river margin (shoal areas), run, rapids, backwater, and main channel (reservoir deep water) areas. No attempt was made to quantify the various habitat types available throughout the 118 km study area. Ranges were defined as the total linear distance (km) between the extreme upstream and downstream locations of each fish. Distances were measured from maps and expressed as total and seasonal ranges. Minimum distance moved was estimated by measuring the total distance (m) between successive locations.

To facilitate movement and habitat use analyses, data was partitioned by river section and season. Seasons were defined as spring (April and May), summer (June to mid-September), fall (mid- September to early November), and winter (early November through March). Wilcoxon rank-sum tests were used to determine if mean ranges differed between seasons and sections (Conover 1971). The relationship between fish length and range was examined by linear regression (Snedecor and Cochran 1980). Kruskal-Wallis tests were used to identify movement differences among seasons and between sections and changes in seasonal depth distribution (Conover 1971). Chi-square tests were used to compare habitat use across seasonal periods (Snedecor and Cochran 1980). All data analyses were performed with Number Cruncher Statistical Systems (Hintze 1995). When comparing measured variables requiring many repetitive statistical tests, the least significant of the *P*-values is presented in the results. Habitat data from Sections 2 and 3 were combined because of small sample size (only 1 fish in Section 2) and reservoir features common to both sections. Fish 482 (Section 2) was excluded from section comparisons for movement and range analyses as it would not have been statistically valid.

Potential muskellunge spawning areas in Section 1 were monitored each spring for spawning activity by visual observation and egg sampling. Visual observations were conducted from 1 to 7 hours after sunset. Spawning was investigated by slowly maneuvering the boat through a spawning area and scanning with hand-held flood lights for muskellunge activity. Muskellunge sightings in a spawning area were documented and referenced as single, paired muskellunge, or actively spawning. In addition, eggs were collected by placing 0.6 x 0.6 m screen covered trays (Gammon 1965) at various locations within a spawning area. Trays were examined for muskellunge eggs every 2 to 3 days. At each muskellunge sighting or egg tray location, the following information was recorded: date, time, water depth, velocity, and water temperature. The presence of mature muskellunge or egg deposition served to verify and define spawning areas. River discharge information was obtained from USGS records and summarized.

Results

Seasonal movement, habitat use, and spawning activity were documented for 12 of the 13 radio tagged muskellunge. During the three year study, 1,505 locations were obtained of which 71% were from open water tracking (Table 1). Monitoring periods for each fish averaged 740 days with a range of 343 to 1,073 days. Differences in length of individual monitoring periods reflected the extended tagging period (2 years) and fish loss. Three of the 13 radio tagged muskellunge were monitored for less than 1 year (Table 1). One fish

Table 1. Summary of tracking histories of radio tagged muskellunge in the Mississippi River, 1990-1993.

Fish frequency number	Sex	Total length (mm)	River section	Date tagged	Date last located	Number of locations	
						Open water	Ice covered
472[a]	M	1,060	1	9 July 1990	3 August 1990	5	-
532	F	1,210	1	16 July 1990	28 June 1993	173	54
472	F	1,000	1	8 August 1990	28 June 1993	169	54
490	M	1,050	1	22 August 1990	30 July 1991	69	18
512	F	1,165	1	22 August 1990	21 May 1992	93	32
482	M	933	2	1 October 1990	26 April 1993	85	46
560	M	986	3	5 June 1991	28 June 1993	64	35
622	F	1,000	3	18 June 1991	28 June 1993	65	33
602	F	1,051	3	18 June 1991	28 June 1993	66	33
520	F	1,040	3	1 July 1991	28 June 1993	60	35
551	F	920	1	5 August 1991	30 June 1993	78	36
572	F	958	1	12 August 1991	28 June 1993	87	36
592	F	940	1	4 September 1991	28 June 1993	58	18

[a]Transmitter recovered from angler caught fish and reused.

(472) was caught and lost to sport fishing 25 days after implantation. Radio transmitter 472 was recovered and reused 5 days later. The location of fish 592 was unknown for 8 months beginning 27 July 1992. The female muskellunge was relocated during routine monitoring of spawning areas on 6 April 1993. One of four males (490) tagged was monitored for 11 months before the radio signal was permanently lost.

Seasonal Movement and Range

Radio tagged muskellunge exhibited distinct seasonal movements, however, the distances and directions traveled within and between each river section, and by individual fish varied. Individuals from all three sections established defined seasonal ranges that varied from 2.7 to 25.2 km during summer and from 0.6 to 8.2 km during winter (Table 2). Mean individual seasonal movements ranged from 122 to 5,261 m (Table 3).

Winter was a period of limited movement, resulting in smaller ranges for all radio tagged muskellunge. Fish used very little of the available river during winter in Sections 1 and 3 (1-5% and 12-17% of the total river length, respectively). Muskellunge inhabiting Section 3 established larger ($P=0.010$) winter ranges (5.9 km mean) than fish in Section 1 (1.4 km mean). Winter movements reflected the differences in ranges with greater activity in Section 3 than in Section 1 ($P=0.023$). Mean distance between locations during winter was 260 m in Section 1 and 965 m in Section 3 (Table 3). Winter ranges overlapped for nine of the radio tagged muskellunge inhabiting Sections 1 and 3. Nine of the 10 study fish tracked for two or more consecutive years returned to the same wintering areas each year. The one exception was Female 602 which used a deep water pool in the riverine stretch of Section 3 during the second winter of tracking.

As muskellunge activity increased during summer, ranges expanded, and movements were less restricted and predictable. Summer ranges for study fish residing in Sections 1 (10.7 km mean) and 3 (11.0 km mean) were similar ($P=0.762$). Summer movements were also similar between Sections 1 and 3 ($P=0.571$), averaging 1,866 m and 1,316 m, respectively. Extremely active individuals spent short periods at a variety of sites throughout a given river section, while more sedentary fish resided for extended periods of time at more localized sites. Study Fish 572 and 592 were the most active averaging 3,524 m and 4,202 m between locations, respectively. In contrast, the most sedentary individual (Fish 532) averaged 463

Table 2. Seasonal ranges and distances between wintering areas and spawning sites for radio tagged muskellunge in the Mississippi River, 1990-1993. Percent of the total river section encompassed by a range is in parenthesis. Total length of the three river sections were: Section 1 - 64 km, Section 2 - 15 km, Section 3 - 39 km.

Fish frequency number	Seasonal ranges (km) Total	Summer	Winter	Distance between wintering areas and spawning sites (km)
		Section 1		
472	18.9 (30)	9.3 (14)	0.8 (1)	1.1
490	8.2 (13)	8.0 (12)	1.2 (2)	0.9
512	25.2 (39)	25.2 (39)	0.6 (1)	13.1
532	9.5 (15)	2.7 (42)	1.6 (3)	5.9
551	7.8 (12)	3.4 (5)	3.0 (5)	12.0
572	15.7 (24)	15.6 (24)	1.1 (2)	0.3
592	-	-	0.7 (1)	-
		Section 2		
482	13.8 (92)	5.4 (36)	8.2 (55)	0.0
		Section 3		
520	30.4 (78)	12.0 (31)	6.6 (17)	22.0
560	33.6 (86)	15.7 (40)	4.5 (12)	25.7
602	34.6 (89)	8.8 (23)	5.9[a](15)	15.6
622	37.5 (96)	7.4 (19)	6.5 (17)	27.0

[a] Average of two distinct winter ranges.

m between locations during the summer. All radio tagged muskellunge in Section 3 established summer ranges that were overlapping and located in the riverine stretch of the section. Eighty-six percent of all muskellunge with defined summer ranges in Section 1 occupied a common range with at least one other muskellunge. On occasion, fish with overlapping summer ranges were observed in proximity to each other, sometimes within 10 m. No directional movement patterns were evident during summer (Figure 3).

Spring and fall were transitional periods coinciding with travel to and from spawning and overwintering areas, resulting in larger mean movements during these seasons (Table 3). Movements associated with these transitional periods were of greater magnitude in Section 3 than Section 1 (spring P=0.008; fall P=0.089). Within river sections, similar mean distances were traveled during spring and fall (Section 3: spring 4,178 m, fall 3,521 m; and Section 1: spring 1,334 m, fall 926 m). Movements during spring and fall also accounted for most of the observed seasonal differences in directional travel. Directional movements were only evident in Section 3 (Figure 3) where all tagged fish moved upstream during spawning and downstream to overwinter. As a group, muskellunge in Section 1 were almost equally split between individuals moving upstream or downstream during spring and fall.

Seasonal differences were also noted within the study sections. The differences detected in seasonal movements were more pronounced within Sections 1 and 3 ($P \leq 0.038$) than in Section 2 (P=0.392). Fish 482 monitored in Section 2 exhibited movements intermediate to fish in Sections 1 and 3, but used a greater percent of the total available river section (Tables 2 and 3). Winter movements within Sections 1 and 3 were more localized than in any other season, although differences between the seasons were not always significant. Winter ranges were distinctly separate from summer ranges for 3 of the 4 muskellunge within Section 3. Conversely, individuals within Section 1 established winter ranges that were either adjoining or contained within the boundaries of their summer range. Winter

Table 3. Mean seasonal movements of radio tagged muskellunge expressed as distance in meters between consecutive contacts in the Mississippi River, 1990-1993.

Fish frequency number	*N*	Mean	*SD*	*N*	Mean	*SD*
		Winter			**Spring**	
			Section 1			
490	21	133	151	26	234	388
512	34	568	1,091	32	2,002	3,553
551	32	336	411	24	1,182	1,839
572	33	226	456	28	1,154	1,269
592	17	256	523	27	1,819	2,837
532	59	178	271	53	1,068	1,554
472	56	122	278	55	1,880	2,316
			Section 2			
482	48	1,060	1,380	28	1,552	2,716
			Section 3			
560	33	513	1,303	17	4,926	8,471
622	32	538	768	16	5,261	7,895
602	31	1,229	2,947	17	2,626	5,372
520	33	1,580	1,587	17	3,898	6,603
		Summer			**Fall**	
			Section 1			
490	20	845	2,043	16	256	243
512	30	1,914	3,006	24	1,767	2,481
551	36	974	794	18	315	397
572	35	3,524	3,096	22	934	1,289
592	15	4,202	4,134	12	1,118	1,205
532	76	463	477	35	827	638
472	70	1,140	1,589	38	1,262	2,111
			Section 2			
482	31	2,215	2,286	18	2,747	3,483
			Section 3			
560	33	1,183	1,848	12	4,627	3,300
622	37	732	1,410	12	4,162	6,137
602	38	659	1,331	11	733	1,057
520	32	2,689	3,543	9	4,562	4,943

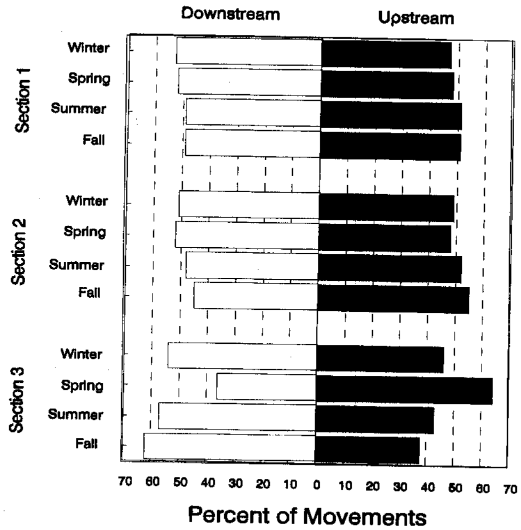

Figure 3. Frequency of seasonal upstream and downstream movements of radio tagged muskellunge in three study sections of the Mississippi River, 1990-1993.

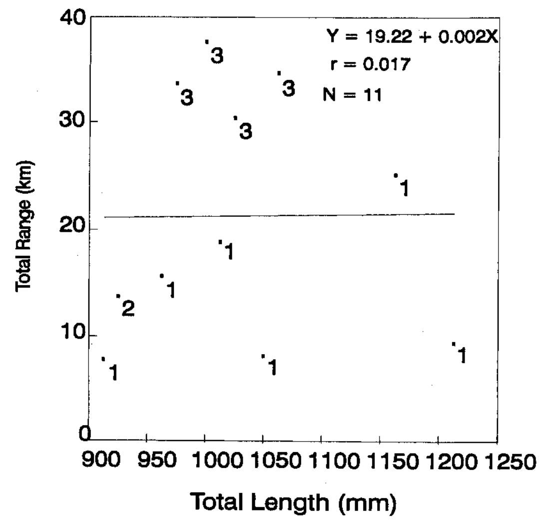

Figure 4. The relationship between fish length and total range size for radio tagged muskellunge in the Mississippi River, 1990-1993. Radio tagged muskellunge in the various river sections are shown as 1, 2, and 3.

ranges were shorter than summer ranges for 10 of the 11 radio tagged muskellunge (P=0.003).

Total ranges were larger for fish inhabiting Section 3 than for fish in Section 1 (P=0.009). Total range varied from 7.8 km to 37.5 km, and averaged 14.2 km in Section 1 and 34.0 km in Section 3 (Table 2). Fish from both Sections 2 and 3 established total ranges that nearly encompassed the entire length of their respective river sections (Table 2). In contrast, muskellunge from Section 1 used less than 40% of the total river available to them (range length 7.8 - 25.2 km). Overlapping of total ranges occurred for 90% of the monitored fish, and ranged from 83% in Section 1 to 100% in Section 3. Fish 512 exhibited the greatest total range in Section 1, overlapping 4 of the 5 other study fish with defined ranges. No relationship between total range length and TL was detected (Figure 4).

The number of locations per individual was greater in Section 1 than in Sections 2 or 3. No valid relationship between total number of locations per individual and range length was found. Fish in Section 1 established short ranges in relation to the available area, while fish in Section 2 and 3 used the whole length of river within their respective sections. In several cases, longer stretches of rapids found in Section 1 during low summer flows may have acted as barriers to muskellunge movements.

Habitat, Cover, and Substrate Use

A variety of habitats were occupied by radio tagged muskellunge throughout the year (P<0.001) in all sections, reflecting the discrete differences in seasonal selection of habitat by individuals. All locations in Section 1 were in riverine habitats, while 59% of all locations in Sections 2 and 3 were associated with reservoir habitats. Mean depths occupied by study fish also had a similar seasonal pattern, while still illustrating the depth differences inherent to the various river sections (Table 4). Mean depth

Table 4. Mean water depth (m) at contact location of radio tagged muskellunge in the Mississippi River, 1990-1993. Within each section, seasons with no letters in common are significantly different.

Season	*N*	Mean	Standard deviation	X^2	*P*
		Section 1		207.63	<0.001
Winter	260	2.5[a]	0.84		
Spring	247	1.6[b]	0.65		
Summer	282	1.6[b]	0.53		
Fall	166	2.0[c]	0.72		
		Section 2		31.52	<0.001
Winter	49	4.1[a]	2.40		
Spring	31	2.6[bc]	2.16		
Summer	32	1.9[c]	0.95		
Fall	19	3.3[ab]	1.82		
		Section 3		210.06	<0.001
Winter	133	3.6[a]	1.14		
Spring	71	1.2[b]	0.63		
Summer	136	1.6[bc]	0.87		
Fall	46	2.1[c]	1.24		

at locations varied from 2.0 to 4.1 m during the fall and winter periods, and from 1.2 to 1.9 m during the spring and summer periods. Muskellunge used deep water habitats more frequently during fall and winter, and depths were greater in winter than in fall ($P<0.050$). Deep water pool and main channel habitats together accounted for 49% of the total locations (Table 5). Shallow water habitats, which includes runs, backwaters, and rapids, were used most frequently (74%) during spring and summer. For all fish combined, depths associated with spring and summer locations were similar, both averaging 1.6 m. River margin was the third most frequently used habitat, accounting for 17% of all locations (Table 5). Use of river margins was not limited to any specific river section, yet greater use of river margins occurred in Sections 2 and 3. Backwater areas were important during the spring spawning period (Table 5), but only accounted for 4% of all locations. Association with rapids was infrequent (1%) and limited to Section 1. The transitional movement of two fish between wintering and spawning areas constituted the majority of locations in rapids.

Muskellunge used a greater diversity of cover types during spring and summer periods in Section 1, than they used in fall (Figure 5). Association with various cover types differed seasonally ($P<0.006$); exceptions were use of open water and bottom morphology ($P<0.16$). A shift away from vegetation toward deep water areas occurred during fall. Muskellunge used timber as cover less frequently during summer than in spring and fall. Visual observations confirmed the use of various cover types (e. g. timber, rocks, and changes in bottom morphology) as current breaks by radio tagged muskellunge. The apparent affinity for specific cover types by individuals also contributed to their frequency of use independent of seasonal patterns.

Muskellunge were located most frequently over sand substrate in Section 1 (Figure 5). Seasonal differences were most evident for locations over sand and silt, where association with silt decreased as the seasons progressed from spring to fall ($P=0.003$). Individuals routinely associated with hard substrates such as gravel, cobble, and boulder throughout the year ($P>0.100$).

Table 5. Seasonal occurrence of radio tagged muskellunge in various habitat types in the Mississippi River, 1990-1993. Percentages for a season are in parentheses.

Habitat type	Winter	Spring	Summer	Fall
		Section 1		
Pool	211 (82)	56 (22)	74 (26)	115 (67)
River margin	3 (1)	41 (16)	78 (27)	27 (16)
Run	45 (17)	119 (47)	123 (43)	29 (17)
Rapids	0 (0)	10 (4)	4 (1)	0 (0)
Backwater	0 (0)	27 (11)	10 (3)	1 (1)
Main channel[a]	0 (0)	0 (0)	0 (0)	0 (0)
		Sections 2 and 3		
Pool	16 (9)	2 (2)	18 (10)	4 (6)
River margin	11 (6)	28 (28)	49 (28)	23 (35)
Run	2 (1)	30 (30)	72 (41)	10 (15)
Rapids	0 (0)	0 (0)	0 (0)	0 (0)
Backwater	0 (0)	23 (23)	3 (2)	0 (0)
Main channel[a]	153 (84)	17 (17)	33 (19)	29 (44)

[a]Deep water

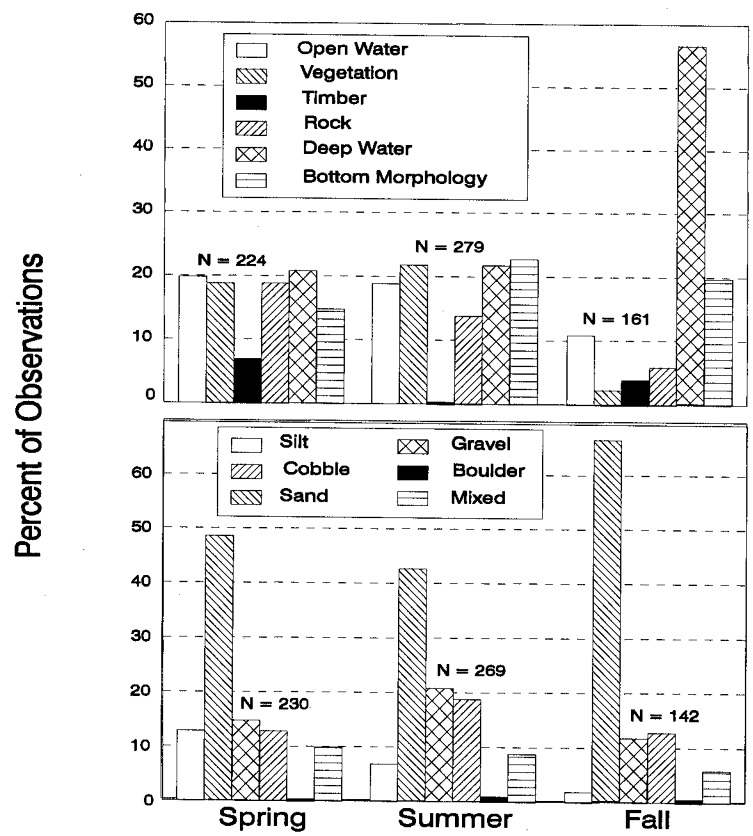

Figure 5. Seasonal association with various cover types (top) and substrate types (bottom) of radio tagged muskellunge in Section 1 of the Mississippi River, 1990-1993.

Spawning Period

Movements from winter ranges to spawning sites began in late March to early April. Distances between winter ranges and spawning sites varied from 0.0 to 27.0 km (Table 2). Mean distances of 5.5 km (SD=5.8) for fish in Section 1 and 21.2 km (SD=8.7) for fish in Section 3 were significantly different (P=0.009). Four fish spawned upstream and three fish spawned downstream of their winter ranges in Section 1. In contrast, all fish in Section 3 used spawning sites upstream of their winter ranges. In Section 2, the only potential spawning site located bordered the winter range of Fish 482.

Seven spawning sites, consisting of 19 distinct spawning areas were located and documented during the study (Table 6). Five

Table 6. Identification and classification (Cowardin et al. 1979) of spawning sites and spawning areas used by muskellunge in the Mississippi River, 1991-1993.

Spawning area	River section	Description	Wetlands system	Classification
		Spawning Site 1		
1A1	1	Side channel	Unknown	Unclassified
		Spawning Site 2		
2A1	1	Island cove	Unknown	Unclassified
		Spawning Site 3		
3A1	1	Finger channel	Palustrine	UBG[a]
3A2	1	Side channel	Riverine	2UBH[b]
3A3	1	Finger channel	Unknown	Unclassified
3A4	1	Side channel	Riverine	2UBH
		Spawning Site 4		
4A1	1	Finger channel	Unknown	Unclassified
4A2	1	Finger channel	Palustrine	SSIC[c]
4A3	1	Island cove	Unknown	Unclassified
4A4	1	Side channel	Palustrine	SSIC
4A5	1	Side channel	Riverine	2UBH
4A6	1	Island cove	Unknown	Unclassified
		Spawning Site 5		
5A1	1	Island cove	Riverine	2UBH
5A2	1	Side channel	Unknown	Unclassified
		Spawning Site 6		
6A1	2	River margin	Unknown	Unclassified
		Spawning Site 7		
7A1	3	Side channel	Palustine	FOIC[d]
7A2	3	Side channel	Palustine	FOIC
7A3	3	Island cove	Palustine	FOIC
7A4	3	Side channel	Palustine	FOIC

[a]UBG - Unconsolidated bottom and intermittently exposed
[b]2UBH - Lower perennial, unconsolidated bottom, and permanently exposed
[c]SS1C - Scrub shrub, broad-leaved deciduous, and seasonally flooded
[d]F01C - Forested, broad-leaved deciduous, and seasonally flooded

spawning sites averaging 1.5 km in length were identified in Section 1, while one spawning site was identified in Section 2 (2.0 km) and one in Section 3 (2.9 km). Each spawning site contained from one to six spawning areas. Spawning areas were fewer and less dispersed in the reservoir sections (Sections 2 and 3) than in Section 1.

Physical characteristics of the 19 areas were similar, except Area 6A1 (Section 2) that was located in river margin habitat. Muskellunge spawning in Sections 1 and 3 used backwater habitats common to riverine stretches of the respective sections. Backwater habitats used for spawning were described as finger channels, side channels, and island coves (Table 6, Figure 6). Spawning areas were initially identified by the sudden change in behavior and movements of radio tagged fish.

Males typically arrived at the spawning area first and lingered the longest. Fidelity to a specific spawning area ranged from 8 to 47 days for the 4 male study fish. Female muskellunge staged near spawning areas prior to entering these areas. Females rarely spent extended periods of time at any one location during the spawning period, choosing instead to frequent multiple areas within the spawning site. All radio tagged muskellunge appeared to spawn annually.

Three of the seven radio tagged muskellunge from Section 1 spawned in at least one of the six spawning areas located in Site 4. Among the other sites in Section 1, two fish used Site 3 and 5, while one fish spawned in Site 1 and Site 2. During two consecutive springs, Fish 592 moved between spawning Sites 3 and 4, which were separated by 2.2 km. In Section 3, three of the four

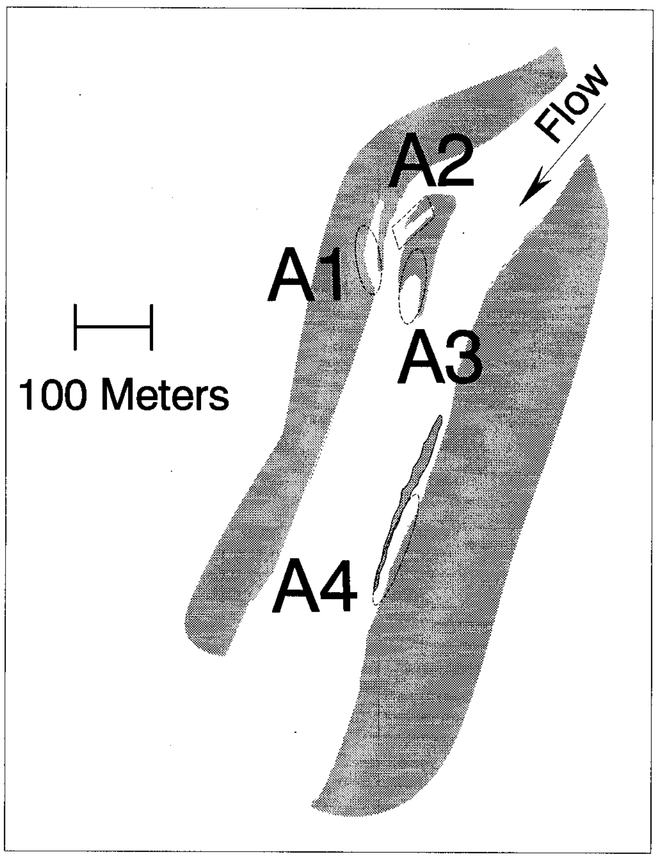

Figure 6. Types of muskellunge spawning areas found in the Mississippi River. Spawning areas include finger channels (A1 and A2), island cove (A3), and side channel (A4).

muskellunge (one male and two females) used the same spawning area (Area 7A1). Fish 602 bypassed Area 7A1 for areas located farther upstream. One behavioral trait common to all study fish was a return to the same spawning site each spring. For seven of the fish, this required bypassing other potential spawning sites closer to their winter ranges and returning to spawning sites used in previous springs.

In Section 1, both radio tagged and untagged muskellunge were observed at spawning areas located throughout the section. Although numerous pairs of males and females were observed in these areas, only three pairs were visually observed spawning. Both night and day spawning was observed, with one visual spawning observation involving radio tagged Fish 490. Muskellunge eggs were first sampled in 1992, although both the effort and egg sample was low (Table 7). By the end of the 1993 spawning period, eggs were collected from all spawning areas in Section 1.

Spawning areas were shallow with a mean depth of 80.6 cm (*SD*=19.1) and consisted of unconsolidated bottoms primarily of muck, silt, and sand covered by senescent or decomposing vegetation. Muskellunge were sighted in the spawning areas at water temperatures ranging between 8.5 and 13.3 °C (10.9 °C mean, *SD*=1.5). These areas also can be characterized as exhibiting low or unmeasurable flow and are seasonally to permanently flooded.

River discharges during the spawning periods were highly variable within and between years (Figure 7). Daily river discharges during the period encompassing 15 April to 15 May averaged 9,123 cfs (*SD*=2,512) in 1991, 7,083 cfs (*SD*=1,900) in 1992, and 8,221 cfs (*SD*=1,461) in 1993. During periods of egg deposition and incubation, daily river discharges declined in 1991 and 1992 although the magnitude of decline was greater and longer in 1992 (Figure 7). In 1993, daily discharges were declining before an influx of water reversed that trend in late April.

Discussion

Radio tagged muskellunge in the Mississippi River exhibited seasonal behavioral differences in both movements and habitat selection. Comparison between river sections revealed that seasonal behavioral changes occurred in each section, although within each section the magnitude of an individual's change was directly affected by the location and quantity of habitat. The most critical habitat needs for muskellunge in the Mississippi River occur in winter and during spawning. In Section 1 (riverine), a greater distance occurs between the dams providing more diverse habitat types for muskellunge to choose from throughout the section. In contrast, Section 3 is shorter and more characteristic of an impounded river (reservoir) and unlike Section 1 has limited riverine habitat available. By our definition,

Table 7. Summary of muskellunge spawning site observations for Section 1 of the Mississippi River, 1991-1993. Standard deviations are in parenthesis.

Year	Monitoring period (days)	Total number of fish	Mean water temperature (°C)	Mean water depth (cm)	Number of eggs collected	Number of egg trays
1991	3	11	10.1 (0.01)	85.8 (14.93)	0	0
1992	5	30	12.3 (2.51)	38.0 -	10	6
1993	9	56	11.1 (1.49)	80.4 (19.12)	213	20

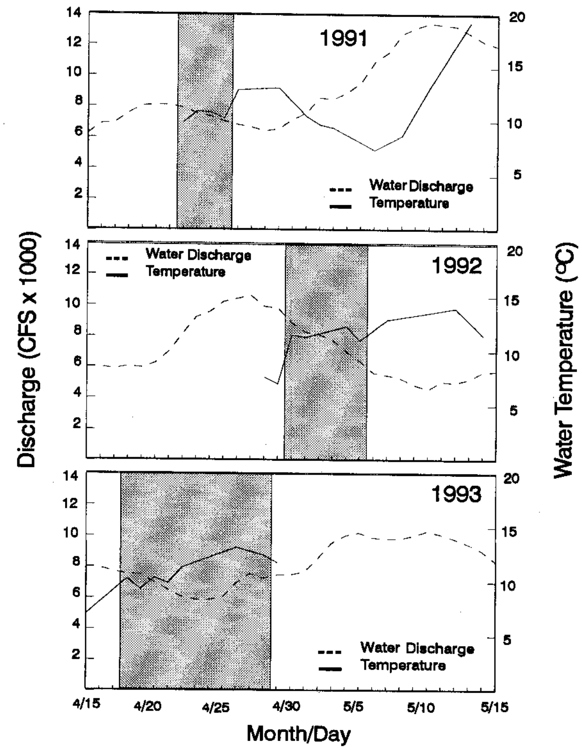

Figure 7. Spawning chronology of muskellunge in Section 1 of the Mississippi River, 1991-1993. Shaded areas represent time periods during which spawning activity and egg deposition were verified.

it appears that the majority of suitable overwintering and spawning habitats only occur in a few select locations of Section 3, and at opposite ends of the river. This observation was supported by the spring and fall dam to dam movement exhibited by radio tagged fish in Section 3, as opposed to riverine section fish that generally ranged less in a given season.

During winter, muskellunge movements were localized within a short range and associated with deep water habitats in all study sections. Although a few deep pools were available in, or near their summer ranges, most muskellunge inhabiting the reservoir section traveled downstream approximately 25 km to overwinter in main channel habitats. The one exception was Fish 602 inhabiting a deep pool similar to the wintering habitat found in Section 1. The finite amount of deep water available to fish inhabiting Section 1 is evident by smaller winter ranges as compared to fish inhabiting the reservoir section. Restricted movements or reduced home ranges of muskellunge during winter have been previously reported for lakes (Dombeck 1979; Minor and Crossman 1978) and Walker Bay of Leech Lake (Strand 1986). Minor and Crossman (1978) reported non-overlapping winter home ranges in Nogies Creek, while neither Strand (1986) nor Dombeck (1979) specifically mentioned overlapping winter ranges. The importance of deep water wintering areas (particularly pools in Section 1) in the Mississippi River was dramatically illustrated by the number of muskellunge with overlapping winter ranges.

Muskellunge from Sections 1 and 3 used spawning areas with similar physical characteristics that were typical of riverine habitats. These areas were found scattered throughout the riverine section but only found downstream of Blanchard Dam (Section 3). This resulted in Section 3 muskellunge moving upstream to reach spawning areas 15-27 km from their overwintering areas, while fish inhabiting Section 1 traveled 13 km or less to spawning habitat. Crossman (1990) suggested that lake area or available stream distance may govern distance traveled by muskellunge to and from spawning areas. However, available habitat rather than river length was the determining factor in governing the distances traveled by muskellunge in the Mississippi River. The dissimilarities previously noted in range of movements between fish inhabiting riverine and reservoir sections supports the assumption that specific habitats, along with availability and location of these habitats, are critical during certain times of the year. In the Mississippi River, spawning sites were near summer ranges in both Sections 1 and 3. Similar to spring, summer activities were most often found in association with riverine habitats. Muskellunge also expanded their range and used a greater variety of shallow water habitats during summer. Investigations of southern riverine systems found muskellunge frequently inhabiting low gradient pools (Axon and Kornman 1986; Monaghan 1985; Brewer 1980; Miles 1978; Parsons 1959) averaging 1.0 to 1.4 m in depth (Axon and Kornman 1986) and associated with fallen trees or boulders (Axon and Kornman 1986; Monaghan 1985). Harrison and Hadley (1978) reported that summer habitat of Niagara River muskellunge was restricted to portions of the river where current velocity reached 1.0 meter per second. Since these results primarily reflect data collected during spring and summer, by using conventional mark and recapture techniques, no attempt to quantify specific habitat use was made. Mississippi river muskellunge increased their movements and ranges during summer, and at times had somewhat disjointed ranges. Similar increases in activity and disjointed home ranges have also been described for other muskellunge populations (Miller and Menzel 1986a; Strand 1986; Dombeck 1979; Minor and Crossman 1978).

The abandoning of a home range during spring or fall for purposes of spawning or establishment of a second home range (winter) was first described by Minor and Crossman (1978) for muskellunge in Nogies Creek Lake. Increased movements of a directed nature during spring and fall were documented for radio tagged muskellunge in Minnesota (Strand 1986), Iowa (Miller and Menzel 1986a), and Wisconsin (Dombeck 1979) lakes. In the Mississippi River, spring and fall were transitional periods when muskellunge were moving between winter and spawning areas, and summer and winter areas. Most Mississippi River muskellunge displayed homing behavior during three distinct seasons: winter, spawning, and summer. Radio tagged fish returned to the same wintering areas in successive years, and in the riverine section these were small and very defined areas. All fish followed for more than one spawning season returned to spawning sites used during previous springs (a maximum of three separate spawning seasons monitored). Mississippi River muskellunge also exhibited homing tendencies during the summer, but summer homing was best described as an attraction to a given river stretch as opposed to a more confined winter range. While most muskellunge displayed very predictable homing behavior each season, there was an occasional fish that would fail to return to a specific area for unknown reasons. Homing by muskellunge during spring (spawning) and summer has been previously documented by Margenau (1994), Crossman (1990), and Miller and Menzel (1986b).

Homing is defined as "the return to a place formerly occupied instead of going to other equally probable places" (Gerking 1959). This definition applies extremely well to the most riverine section that we studied. In Section 1, there were a variety of similar habitats available seasonally, but individuals predictably returned to formerly occupied areas bypassing other probable places. In contrast, Section 3 fish behaved almost as a group, moving upstream during spring and downstream in fall, to satisfy their seasonal habitat needs. Movement as a group would suggest that a limited amount of suitable habitat is present in Section 3 resulting in extended movements and predictable homing behavior.

Shallow, low flow backwater habitats were identified as the primary spawning habitat of muskellunge in the Mississippi River. In the absence of suitable backwater areas (Section 2), muskellunge appear to use river margin habitat for spawning. Various physical characteristics associated with these areas differed from other riverine studies, but were comparable in many ways to spawning habitats described for lacustrine systems. Stream studies in Kentucky (Brewer 1980), West Virginia (Miles 1978), and Tennessee (Parsons 1959) reported spawning to occur in low gradient, shallow water areas associated with the upper or lower ends of pools. In North Carolina rivers, Monaghan (1985) subjectively identified spawning habitat as slow moving low gradient tributary streams, or eddies or still areas below instream structure (boulders, sandbars, trees and island). Descriptions of spawning areas in larger riverine systems ranged from shallow bays with little current in the St. Lawrence River (Dombeck 1986) to main river areas with current velocities of 0.2 meters per second in the Niagara River (Harrison and Hadley 1978). Spawning in these river systems occurred from late March through May at water temperatures ranging from 10 to 15 °C. Spawning substrates ranged from hard surfaces (rock, rubble, gravel, or bedrock) rarely or occasionally associated with vegetation (Osterberg 1985; Brewer 1980) to soft surfaces (sand or silt) associated with vegetation or organic material (Parsons 1959; Monaghan 1985). Similarly, spawning activity in lakes has been described as occurring in shallow water (< 1 m) and over muck and sand substrates with dead vegetation (Dombeck 1979) or matted vegetation and leaf litter (Minor and Crossman 1978). Upstream of our study area, in a Mississippi River headwaters reservoir (Leech Lake), Strand (1986) identified muskellunge spawning areas as deep (1-2 m) open water areas with flocculent marl substrates and dense beds of *Chara* spp. These open water spawning areas differed from the traditional description (Scott and Crossman 1973), but more closely resembled areas described by Haas (1978) in Lake St. Clair, Michigan. In an attempt to summarize existing information concerning muskellunge spawning habitat, Dombeck et al. (1984) concluded that different waters provided different types of spawning habitat.

The impact of variations in river discharge on muskellunge spawning success is largely unknown. Brewer (1980) found low discharges coupled with seasonable water temperatures favorable, and high discharges and low water temperatures unfavorable for muskellunge reproductive success in Kentucky streams. When addressing lake impoundments, Dombeck et al. (1986) suggested that rising springtime water levels were beneficial for muskellunge reproductive success, while stable water levels appeared detrimental to muskellunge reproduction. For spawning areas in the Mississippi River, discharge appears to play a critical but undefined role in reproductive success of muskellunge. Each spring, muskellunge in the Mississippi River were confronted with changing river conditions as they returned to the same spawning areas. These areas were typically located in backwater habitats outside the direct influence of the main river. Minor fluctuations in daily river discharges appeared to have little impact on spawning habitat or behavior. However, rapidly declining water levels appeared to reduce available spawning habitat, while rising water levels laterally shifted the available spawning area. Under extreme high flow conditions, fish returning to a spawning area were forced to move laterally into recently flooded adjacent areas and away from the influence of increased flows affecting the principal spawning area. Rapidly rising or falling water levels also poses a problem for incubating eggs and developing sac-fry through flushing or dewatering of spawning areas.

Males and female muskellunge spawning in the Mississippi River differed in their arrival and departure time, and faithfulness to one spawning area. Minor and Crossman

(1978) and Strand (1986) reported similar observations in lakes. This suggests that both sexes may spawn with multiple partners thus maintaining a broader gene pool. In addition, Dombeck (1979) observed spawning during the night, while Minor and Crossman (1978) reported spawning activity only occurred during daylight hours. Based on visual observations in the Mississippi River, spawning occurred both day and night. Strand (1986) reported that both sexes were sensitive to drastic changes in weather, temporarily moving off the spawning areas during severe cold fronts. During the beginning of the 1993 spawning period, a cold front caused water temperatures in the river to fluctuate, resulting in an extended spawning period in comparison to the previous two years. Both day and night spawning activity was observed in 1993, suggesting that interruptions that extend the spawning period may in turn have caused changes in muskellunge spawning behavior.

Management Implications

Identification of seasonal habitat requirements for all muskellunge life stages is required to assure the integrity of the habitat and perpetuation of a self-sustaining population. Two key habitats were identified as critical and limiting for muskellunge populations in the Mississippi River. Backwater areas are essential for muskellunge spawning and require protection from shoreline development and disturbance to the riparian zone. Backwaters are used by the same fish each year repetitively, further emphasizing their importance. The importance of deep water habitats during winter was illustrated in all river sections, and should be protected. Any habitat alterations reducing the quantity or quality of deep water habitat could influence the overall survival and abundance of the population. Because of differences in the quantity of human development on various sections of the Mississippi River, habitat management strategies will need to address the problems unique to each section.

Peak river discharges typically occur in April and coincide with muskellunge spawning. Once the spawning temperature threshold is reached an additional 18 to 24 days are required for egg and fry development. High water levels during this period can be both beneficial and disastrous to reproductive success. Increased water levels during spring are essential for establishing backwater areas that are seasonally flooded and serve as both spawning and nursery areas. However, rapidly changing water levels during spawning, or egg and fry development periods, could severely impact reproductive success. Water levels should remain relatively stable during these critical early life history periods. Additional studies should be conducted to determine the impact of fluctuating discharges on muskellunge reproductive success and early life history.

How specific habitats limit muskellunge populations in the Mississippi River is unknown, and was not evaluated as part of the current study. However, seasonal behavioral patterns suggest that spawning habitat is limiting in the reservoir sections and wintering areas are limiting in the riverine section. Further investigations are required to determine to what degree these habitats restrict muskellunge populations in riverine systems.

REFERENCES

Axon, J. R., and L. E. Kornman. 1986. Characteristics of native muskellunge streams in eastern Kentucky. American Fisheries Society Special Publication 15:263-272.

Brewer, D. L. 1980. A study of native muskellunge populations in eastern Kentucky streams. Kentucky Department of Fish and Wildlife Resources, Fisheries Bulletin Number 64, Frankfort.

Carlander, K. D., J. S. Campbell, and R. J. Muncy. 1978. Inventory of percid and esocid habitat in North America. American Fisheries Society Special Publication 11:27-38.

Conover, W. J. 1971. Practical nonparametric statistics. John Wiley and Sons Inc., New York.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. Fish and Wildlife Service, U.S. Department of the Interior, Office of Biological Services Report Number FWS/OBS-79/31.

Crossman, E. J. 1977. Displacement and home range movements of muskellunge determined by ultrasonic tracking. Environmental Biology of Fishes 1:145-158.

Crossman, E. J. 1986. The noble muskellunge: A review. American Fisheries Society Special Publication 15:1-13.

Crossman, E. J. 1990. Reproductive homing in muskellunge, *Esox masquinongy*. Canadian Journal of Fisheries and Aquatic Sciences 47:1803-1812.

Dombeck, M. P. 1979. Movement and behavior of the muskellunge determined by radio-telemetry. Wisconsin Department of Natural Resources Technical Bulletin Number 113, Madison.

Dombeck, M. P. 1986. Muskellunge habitat with guidelines for habitat management. American Fisheries Society Special Publication 15:208-215.

Dombeck, M. P., B. W. Menzel, and P. N. Hinz. 1984. Muskellunge spawning habitat and reproductive success. Transactions of the American Fisheries Society 113:205-216.

Dombeck, M. P., B. W. Menzel, and P. N. Hinz. 1986. Natural muskellunge reproduction in midwestern lakes. American Fisheries Society Special Publication 15:122-134.

Gerking, S. D. 1959. The restricted movements of fish populations. Biological Review 34:221-242.

Gammon, J. R. 1965. Device for collecting eggs of muskellunge, northern pike, and other scatter-spawning species. The Progressive Fish-Culturist 27:78.

Haas, R. C. 1978. The muskellunge in Lake St. Clair. American Fisheries Society Special Publication 11:334-339.

Hanson, D. A., J. R. Axon, J. M. Casselman, R. C. Haas, A. Schiavone, and M. R. Smith. 1986. Improving muskie management: A review of management and research needs. American Fisheries Society Special Publication 15:335-341.

Harrison, E. J., and W. F. Hadley. 1978. Ecologic separation of sympatric muskellunge and northern pike. American Fisheries Society Special Publication 11:129-134.

Hintze, J. L. 1995. Number cruncher statistical system. Kaysville, Utah.

Margenau, T. L. 1994. Evidence of homing of a displaced muskellunge, *Esox masquinongy*. Journal of Freshwater Ecology 9(3):253-256.

Miles, R. L. 1978. A life history of the muskellunge in West Virginia. American Fisheries Society Special Publication 11:140-145.

Miller, M. L., and B. W. Menzel. 1986a. Movement, activity, and habitat use patterns of muskellunge in West Okoboji Lake, Iowa. American Fisheries Society Special Publication 15:51-61.

Miller, M. L., and B. W. Menzel. 1986b. Movements, homing, and home range of muskellunge, *Esox masquinongy*, in West Okoboji Lake, Iowa. Environmental Biology of Fishes 16:(4)243-255.

Minor, J. D., and E. J. Crossman. 1978. Home range and seasonal movements of muskellunge as determined by radiotelemetry. American Fisheries Society Special Publication 11:146-153.

Monaghan, J. P., Jr. 1985. A study or riverine muskellunge populations and habitat in North Carolina. Division of Boating and Inland Fisheries, North Carolina Wildlife Resource Commission, Federal Aid in Fish Restoration Project F-24-95, Raleigh.

Osterberg, D. M. 1985. Habitat partitioning by muskellunge and northern pike in the international portion of the St. Lawrence River. New York Fish and Game Journal 32:159-166.

Parsons, J. W. 1959. Muskellunge in Tennessee streams. Transactions of the American Fisheries Society 88:136-139.

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

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

Snedecor, G. W., and W. G. Cochran. 1989. Statistical methods, 8th edition. Iowa State University Press, Ames.

Strand, R. F. 1986. Identification of principal spawning areas and seasonal distribution and movements of muskellunge in Leech Lake, Minnesota. American Fisheries Society Special Publication 15:62-73.

White, W. J., and R. J. Beamish. 1972. A simple fish tag suitable for long-term marking experiments. Journal of the Fisheries Research Board of Canada 29:339-341.