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Movements of Adult Lake Sturgeon in the Lake Winnebago System

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Abstract

We used data from a long-term tagging program to analyze movement patterns of adult lake sturgeon (*Acipenser fulvescens*) in the Lake Winnebago system, Wisconsin. Of 13,549 adult lake sturgeon tagged between 1952 and 1984, 1,633 were recaptured at least once. The spatial and temporal distribution of tagging and recapture reflected the distribution of sampling effort as well as the distribution of lake sturgeon. Most fish recaptured in Lake Winnebago had also been tagged there, but usually not in the same area of the lake. Many fish from Lake Winnebago moved into the Wolf River during the spring to spawn, whereas others moved into the Fox or Embarrass rivers. Lake sturgeon from Lake Poygan also moved into the Wolf River during the spring to spawn. Males tended to spawn every 1 or 2 years and females every 3 or 4 years; most of the fish caught on the spawning grounds were males. Most spawning fish returned to the same area of river each time they spawned. Few fish moved between rivers. Adult lake sturgeon were captured in the Wolf River during the fall as well as the spring. Some of the fall-captured fish might have been permanent residents, but others appeared to be fish from Lake Winnebago that moved into the river during the fall and remained there until they were finished spawning in the spring. Our analyses support the belief that little intermixing occurs between lake sturgeon from Lake Winnebago and Lake Poygan. Relatively few lake sturgeon moved between the 2 lakes, and fish from each lake tended to spawn in different areas. Thus, lake sturgeon populations in Lake Winnebago and Lake Poygan should continue to be managed separately.

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PHOTO: JIM KEMPINGER

*Lake Sturgeon spawning
in the Wolf River.*

Introduction

The Lake Winnebago system of Wisconsin contains one of the largest sport fisheries for lake sturgeon (*Acipenser fulvescens*) remaining in the world. To preserve and improve this fishery, as well as to learn more about the biology of the species, Wisconsin Department of Natural Resources (DNR, formerly Wisconsin Conservation Department) biologists have conducted many studies of lake sturgeon in the Lake Winnebago system (Schneberger and Woodbury 1944; Probst and Cooper 1955; Priegel and Wirth 1975, 1977, 1978; Folz et al. 1983; Ceskleba et al. 1985; Folz and Meyers 1985; Wang et al. 1985; Kempinger 1988). These studies have focused on population dynamics, spearing harvest and exploitation, age and growth, food habits, spawning and early life history, and culture of eggs and young. One facet of the biology of lake sturgeon in the Lake Winnebago system that has thus far received relatively little published attention is patterns of movement by adults.

The conclusions of existing published reports on adult lake sturgeon movements in the Lake Winnebago system can be summarized as follows. Many adult fish from Lakes Winnebago, Poygan, Big Butte des Morts, and Winneconne move into the Wolf or Fox rivers during the spring to spawn. After spawning, these fish return to their respective lakes. Lake Sturgeon have been reported to spawn on rocky shores in Lake Winnebago, but this has never been verified. Fish move about within each lake but rarely move between lakes. Male fish make the spawning migration every year or every other year, whereas females only run up the rivers every 3 to 6 years.

Individual fish return to the same location within the river each time they spawn (Probst and Cooper 1955; Priegel and Wirth 1977, 1978; Folz and Meyers 1985).

Some of the movement patterns described above are characteristic of lake sturgeon populations in other locations. For example, studies have found that adults may migrate, sometimes for long distances, up rivers in order to spawn (Harkness and Dymond 1961, Scott and Crossman 1973, Baker 1980). Males tend to make this migration more frequently than females (Roussow 1957, Scott and Crossman 1973), and homing is evident among some spawning fish (Magnin and Beaulieu 1960, Harkness and Dymond 1961).

While these movement patterns appear to be typical of all lake sturgeon populations, other aspects of lake sturgeon movement in the Lake Winnebago system may be unique. For instance, the reported lack of movement between lakes by sturgeon that share the same spawning rivers has not been documented in other basins. This pattern of movement, if real, is evidence for the existence of separate, isolated populations or stocks of lake sturgeon in the Lake Winnebago system, which has important management implications.

Despite limited published information on the movement of lake sturgeon in the Lake Winnebago system, biologists have long been interested in the subject and have collected extensive data that can be used to analyze movement. Since 1952, over 13,000 lake sturgeon in the Lake Winnebago system have been marked with numbered tags that allow recognition of individual fish. Many of these fish

have been recaptured after tagging, and the location and date of each recapture have been noted. Some of these tag-recapture data were collected specifically to look at lake sturgeon movement, but most were collected to determine population size, mortality, and exploitation. Nonetheless, these data are potentially useful in discerning patterns of lake sturgeon movement.

Our objectives were to use these tag-recapture data to examine the validity of current theories about adult lake sturgeon movement in the Lake Winnebago system and to try to answer questions that remain unresolved about patterns of movements. For management purposes, 2 of the more important of these unresolved questions are: (1) Do some adult lake sturgeon remain in the spawning rivers year-round? In other parts of Wisconsin some populations are restricted to rivers (Priegel 1973, Becker 1983, Thuemler 1985). (2) Do lake sturgeon from different lakes use different areas for spawning? We recognize that, because most tag-recapture data were not collected to look at movement, existing data may be insufficient to conclusively answer the 2 questions. Thus, another of our objectives was to determine what future efforts are needed to address these and other questions about lake sturgeon movements.

Study Area

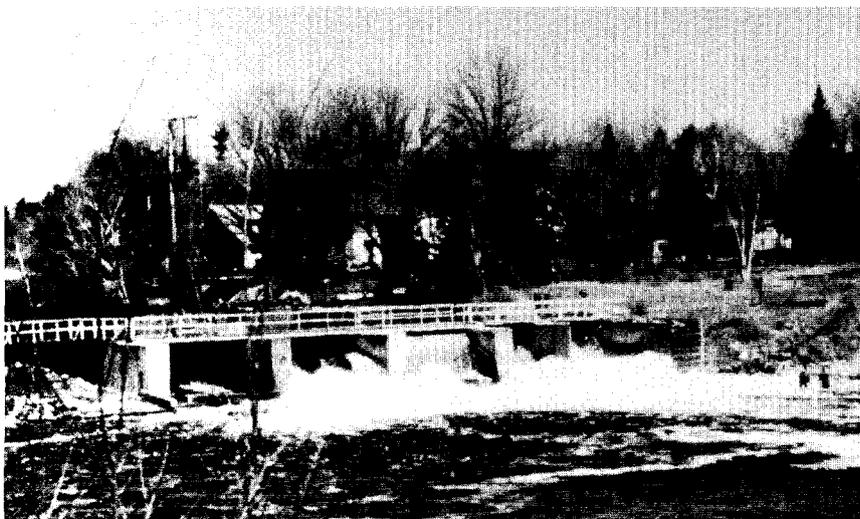
The Lake Winnebago system, as defined for this study, consists of Lake Winnebago, Big Lake Butte des Morts and its connection with Lake Winnebago (hereafter referred to as Lake Butte des Morts), the Fox River between Lake Butte des Morts and the

dam at Eureka, Lake Winneconne and Lake Poygan, the Wolf River between Lake Poygan and the dam at Shawano, and tributaries of the Wolf from their junction with the Wolf up to their source or the point at which a dam blocks upstream passage (Fig. 1). Within the Lake Winnebago system, as we have defined it, there are no physical barriers to fish movement. The 4 major lakes in the system, Lakes Winnebago, Butte des Morts, Winneconne, and Poygan, are all large, relatively shallow, and biologically productive. Neenah Dam, at the Fox River outlet from Lake Winnebago, controls the water level of all 4 lakes. Further details on the physical, chemical, and biological characteristics of the Lake Winnebago system are found in Priegel and Wirth (1975, 1978) and Folz and Meyers (1985).

Methods

All analyses were based on tagging and recapture data for large (> 30 inches total length) lake sturgeon tagged since 1952. For convenience, we refer to all tagged fish as "adults," although some of the smaller individuals were not sexually mature (Priegel and Wirth 1977). Fish were tagged with numbered tags that allowed recognition of individual fish, and the date and location of tagging and each subsequent recapture were noted. A variety of tag types were used; most were Monel "ear" tags, Monel jaw tags, or plastic dart tags. In rivers, fish were captured for tagging with dip nets during the spring spawning run and with electroshockers during the fall. In lakes, fish were captured mainly with gill nets, trap nets, and trawls. Recaptures were made with similar gears in each habitat, except that many recaptures in lakes came from compulsory registration of fish taken by spearing during the winter.

For each tagged lake sturgeon, the following data, if known or applicable, were available in a computer database: total length, weight, age, maturity (mature or immature), sex, type of tag(s) (some fish received more than one tag), tag number, location of tagging, date of tagging, method of capture for tagging, location of recapture, date of recapture, method of recapture, and spearer's license number (if the fish was recaptured by a spearer). We accessed and



One of the major sampling sites during spawning was in the Wolf River at Shawano Dam, 126 miles upstream from Lake Winnebago.

analyzed these data using the Statistical Analysis System (SAS Inst. Inc. 1982).

Lake sturgeon were tagged or recaptured from 158 different locations in the Lake Winnebago system. To simplify the task of analyzing the movement of fish, we condensed these 158 locations into 17 reference areas, 6 each for the Wolf River and Lake Winnebago, and one each for Lake Butte des Morts, Lake Winneconne, Lake Poygan, the Fox River, and the Embarras River (Fig. 1).

We based our analyses of movement on recaptures of tagged fish made between 1954 and 1985. We did not use the following data:

1. Recaptures of lake sturgeon with an unknown tag date or location or an unknown recapture date or location.
2. Recaptures of lake sturgeon made within 30 days of tagging or recapture and within the same area where that tagging or recapture had been made (to avoid multiple observations in the same area during intensive sampling programs).
3. Recaptures of 5 lake sturgeon that were manually transported from Lake Poygan or the Wolf River to Lake Winnebago during the 1960s.

Results

Tagging and Recaptures: Temporal and Spatial Patterns

Between 1952 and 1984, 13,549 adult lake sturgeon were tagged in the Lake Winnebago system. All but 25 of these fish were tagged between 1952 and 1963 (36%) or between 1975 and 1984 (64%).

Tagging of lake sturgeon was seasonal. Most fish were tagged during spring (April-May, 54%) or fall (September-October, 26%). Relatively few were tagged during mid-summer or late winter.

Tagging occurred mainly in 3 bodies of water: Lake Winnebago (51%), Lake

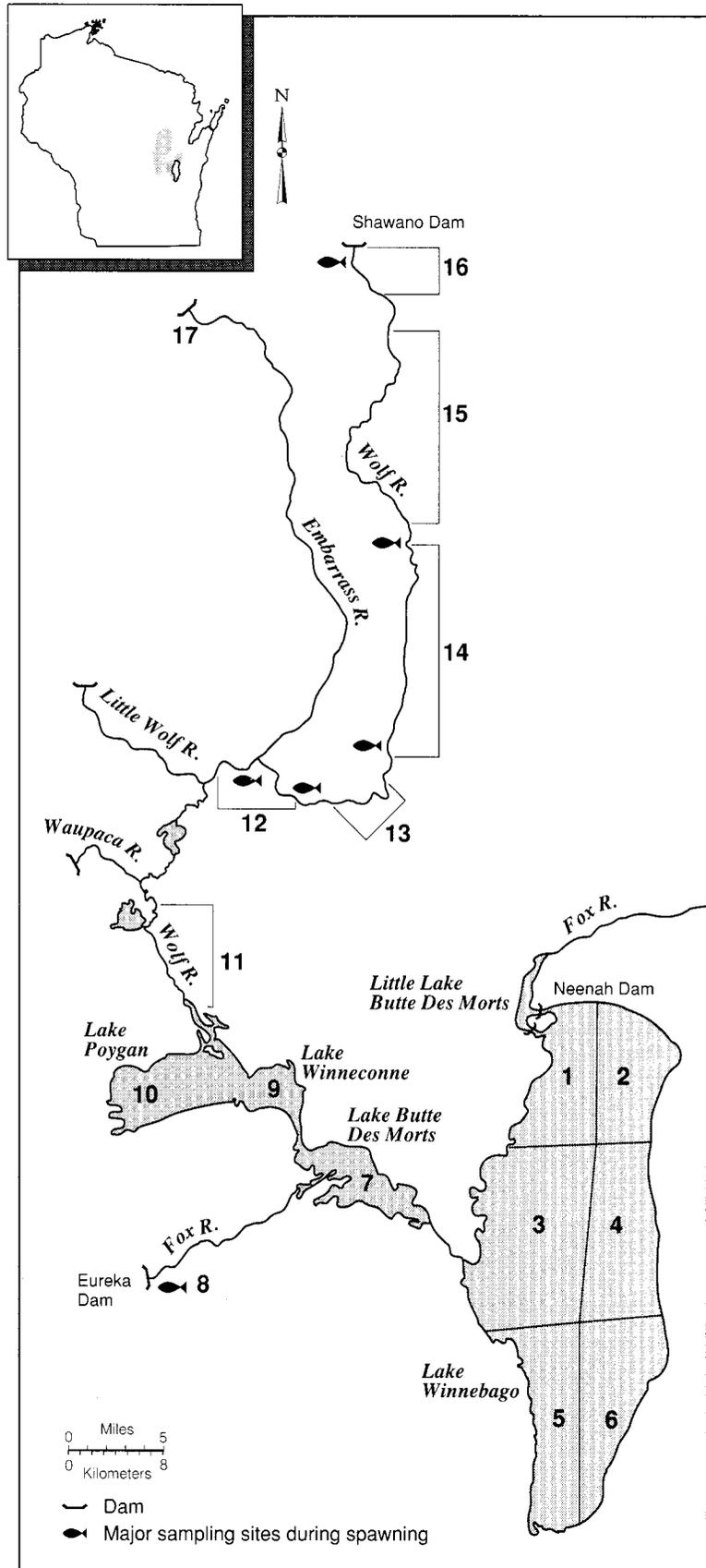
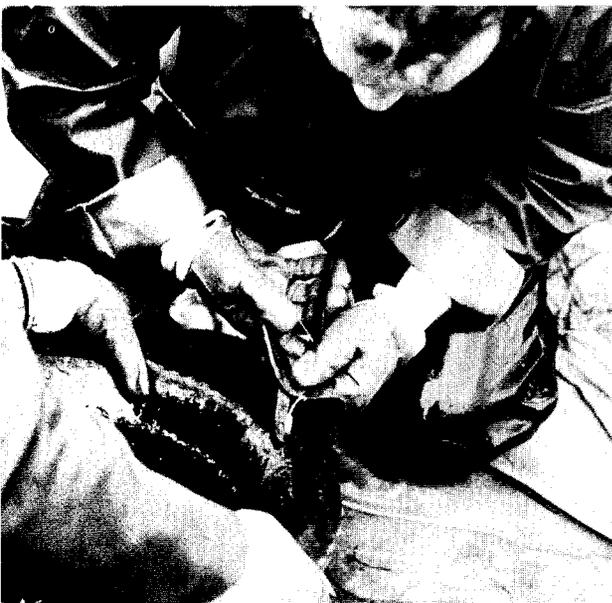
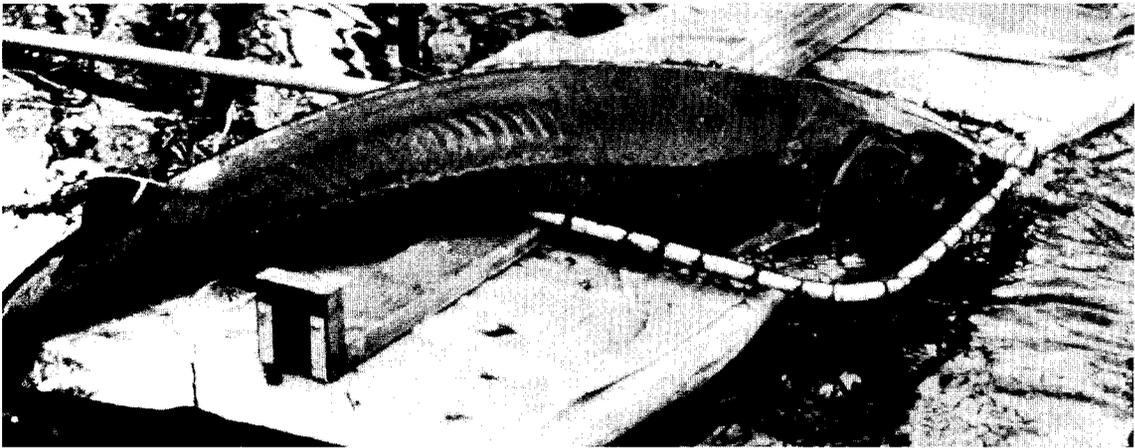


FIGURE 1. The Lake Winnebago system, showing areas used in analyses of tag-recapture data and major sampling sites during spawning.



In rivers lake sturgeon were captured for tagging with dip nets during the spring spawning season.

After netting, all sturgeon were measured and examined for tags.



Monel numbered "ear" tags, here attached to the dorsal fin, allowed identification of individual lake sturgeon. The date and location of tagging and each subsequent recapture were noted in the data used for this study.

Table 1. Number of lake sturgeon tagged and recaptured between 1952 and 1985 in each of 17 areas in the Lake Winnebago system. Recaptures include multiple recaptures of the same fish.

Location (Area)	Tagged Fish		Recaptures	
	No.	Percent (%)	No.	Percent (%)
Lake Winnebago (1)	696	5	244	14
Lake Winnebago (2)	1,099	8	247	14
Lake Winnebago (3)	740	5	82	5
Lake Winnebago (4)	1,592	12	262	15
Lake Winnebago (5)	661	5	141	8
Lake Winnebago (6)	2,092	15	340	19
Lake Butte des Morts (7)	17	<1	1	<1
Fox River (8)	404	3	49	3
Lake Winneconne (9)	8	<1	5	<1
Lake Poygan (10)	1,960	14	56	3
Wolf River (11)	191	1	11	<1
Wolf River (12)	1,255	9	109	6
Wolf River (13)	209	2	11	<1
Wolf River (14)	65	<1	11	<1
Wolf River (15)	574	4	70	4
Wolf River (16)	1,810	13	163	9
Embarrass River (17)	176	1	4	<1
Total	13,549	100	1,806	100

Poygan (14%), and the Wolf River (30%). Within Lake Winnebago most fish were tagged in areas 4 and 6, and within the Wolf River most were tagged in areas 12 and 16 (Table 1). Some lake sturgeon were tagged in Lakes Butte des Morts and Winneconne and the Embarrass and Fox rivers, but none were tagged in the Little Wolf River or the Waupaca River, although lake sturgeon are known to spawn there (Lee Meyers, Wis. Dep. Nat. Resour., pers. comm.).

Tagging was neither random nor regular with regard to location, date, or method of capture. For example, excluding area 11 of the Wolf River, over 85% of the lake sturgeon tagged in rivers were captured after 1975, during the spring with dip nets. Dip netting sites were chosen based on numbers of sturgeon present and ease of sampling. Conversely, nearly all fish (97%) in area 11 of the Wolf River and in Lakes Butte des Morts, Winneconne, and Poygan were tagged during the fall or winter (October through February), after being caught in trap nets or gill nets (Priegel and Wirth 1978). Most fish in Lake Winnebago were tagged during the open-water period (approximately April through November), after being captured in trawling and trap-netting operations designed to remove rough fish (Priegel 1971).

From April 1954 through February 1985, 1,633 different tagged lake sturgeon were recaptured, representing 12% of those that were tagged. Of these 1,633 fish, 1,479 were recaptured only once, 138 were recaptured twice, 13 were recaptured 3 times,

and 3 were recaptured 4 times, for a total of 1,806 recapture observations. Of the 1,633 recaptured at least once, 545 were killed by spearing during the first recapture, leaving a maximum of 1,088 available to be recaptured more than once. Of these 1,088, 154 (14%) were recaptured a second time. Using similar corrections for spearing, 16 out of a possible 105 (15%) were recaptured a third time, and 3 out of a possible 12 (25%) were recaptured a fourth time.

The distribution of recaptures among areas was similar to that of taggings, with a few exceptions (Table 1). Most recaptures occurred in Lake Winnebago (73%) or the Wolf River (21%), but relatively few came from Lake Poygan (3%). A total of only 59 recaptures (3%) came from Lakes Winneconne and Butte des Morts and the Fox and Embarrass rivers. A total of 4 fish, not included in these analyses, were recaptured in northern Green Bay or in Lake Erie (Priegel and Wirth 1977).

As was the case with tagging, recaptures were neither random nor regular with regard to location, date, or method of capture. Generally the methods, times, and locations of recaptures were similar to those of tagging. The main exception was in Lake Winnebago, where nearly all tagging occurred during the open-water season with trap nets and trawls, but almost half of the recaptures were taken by spearing while the lake was ice-covered. Many of the recaptures in Lakes Poygan and Winneconne were also made with spears.

Movement

Most lake sturgeon tagged in Lake Winnebago were recaptured in Lake Winnebago (Tables 2, 3, 4). Tagged fish moved around within Lake Winnebago and typically did not stay within one area of the lake (Fig. 2).

Many lake sturgeon moved in and out of Lake Winnebago (Tables 2, 3, 4). Of the 1,073 recaptures made of fish tagged in Lake Winnebago, 145 (14%) were made outside the lake and of the 732 recaptures of fish tagged outside the lake, 387 (53%) were made in Lake Winnebago. Lake sturgeon tagged in Lake Winnebago were recaptured in the Wolf, Fox, and Embarrass rivers, and lake sturgeon tagged in these rivers were recaptured in Lake Winnebago (Table 2).

Lake sturgeon that were recaptured more than once tended to be recaptured mainly in Lake Winnebago, no matter where they were tagged (Tables 3, 4). In part, this tendency may have been an artifact of the large amount of sampling effort that Lake

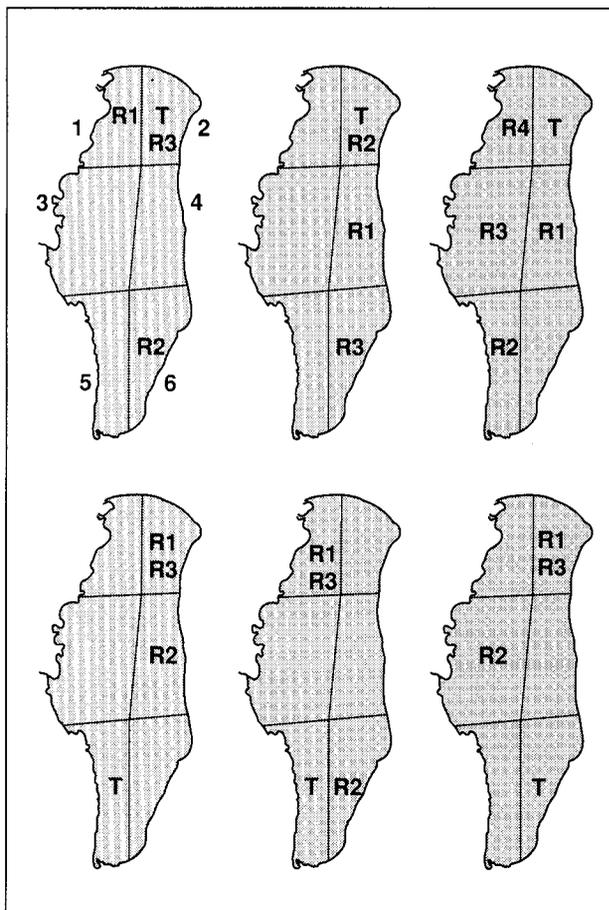


FIGURE 2. Areas of tagging and recapture for lake sturgeon tagged and subsequently recaptured 3 or 4 times in Lake Winnebago. Numbers around map at upper left identify areas; T indicates that tagging occurred in the area, R1 indicates that a first recapture occurred in the area, R2 indicates a second recapture, etc.

Winnebago received, assuming that sampling effort is at least roughly proportional to the sum of tagged and recaptured lake sturgeon at a location. However, it probably also indicates that most lake sturgeon in the Lake Winnebago system ultimately spent at least some time in Lake Winnebago. Fish tagged in the Fox River would appear, at first glance, to be an exception to the above pattern; of the 9 fish tagged there with multiple recaptures, 8 were recaptured only in the Fox River (Table 3). However, among fish tagged in the Fox River with only one recapture, 57% were recaptured in Lake Winnebago and 37% were recaptured in the Fox River. These results probably reflect a strong homing tendency by lake sturgeon during spawning in the Fox River rather than limited movement by lake sturgeon between the Fox River and Lake Winnebago.

Many lake sturgeon moved between Lake Winnebago and the Wolf River (Tables 2, 3, 4). In particular, many moved between area 16 of the Wolf River and area 6 of Lake Winnebago (Table 2). The large number of lake sturgeon tagged and recaptured in these 2 areas probably reflects, in part, the large amount of sampling effort each area received (Folz and Meyers 1985). Nonetheless, lake sturgeon seemed more likely to move between area 6 and area 16 than between area 6 and area 12 of the Wolf, which also received relatively high sampling effort (Folz and Meyers 1985).

Lake sturgeon moved little between rivers, and fish captured (either for the first time or as a recapture) in one area of a river were more likely to be recaptured again in the same area than in another river area (Tables 2, 5). This was particularly true for lake sturgeon captured in the Fox River; 95% of subsequent recaptures of these fish from within rivers were made in the Fox River. Ninety-two percent of the subsequent recaptures from rivers for fish captured in area 12 of the Wolf River were made in area 12, and 68% of the subsequent recaptures from rivers for fish captured in area 16 of the Wolf were made in area 16. The percentage for area 16 increased to 80% when only spring spawning was considered (Table 5). All captures of lake sturgeon in the Fox River and in area 12 of the Wolf River occurred during the spring spawning period.

Spawning Periodicity

Assuming that all lake sturgeon captured at a major sampling site on the Fox or Wolf rivers (Fig. 1) during the spring spawning period were spawning, then some fish spawned every year, while others may have spawned at less frequent or irregular intervals (Table 6). For males, the modal interval between captures during spawning was 2 years, the median

TABLE 2. Capture areas for tagged lake sturgeon that were recaptured at least once. Recaptures include multiple recaptures of the same fish.

Tagging Location (Area)	No. Recaptured, by Area																	Total
	Winnebago (1)	Winnebago (2)	Winnebago (3)	Winnebago (4)	Winnebago (5)	Winnebago (6)	Winnebago (7)	Butte des Morts (8)	Fox (9)	Winneconne (10)	Poygan (11)	Wolf (12)	Wolf (13)	Wolf (14)	Wolf (15)	Wolf (16)	Embarrass (17)	
Lake Winnebago (1)	18	32	4	17	7	28	1	0	0	1	0	2	0	0	6	4	0	120
Lake Winnebago (2)	31	30	14	42	6	26	0	0	0	1	0	0	0	0	2	0	0	152
Lake Winnebago (3)	13	18	3	24	8	33	0	3	0	1	0	6	0	1	4	5	2	121
Lake Winnebago (4)	34	31	9	41	11	46	0	5	0	0	0	3	1	1	3	9	0	194
Lake Winnebago (5)	29	22	4	25	4	25	0	0	0	0	1	1	1	0	0	3	0	115
Lake Winnebago (6)	58	48	21	59	34	74	0	1	0	0	0	7	1	1	12	55	1	372
Lake Butte des Morts (7)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fox River (8)	11	4	1	8	5	9	0	39	0	0	0	3	0	0	0	1	0	81
Lake Winneconne (9)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lake Poygan (10)	7	16	1	12	1	6	0	0	3	37	5	6	0	1	3	3	0	101
Wolf River (11)	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	0	4
Wolf River (12)	18	17	0	6	1	21	0	0	1	6	0	70	5	3	1	8	0	157
Wolf River (13)	2	4	0	2	1	0	0	0	0	2	0	1	1	1	3	0	0	17
Wolf River (14)	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2
Wolf River (15)	4	4	2	1	0	1	0	0	0	1	0	0	1	1	19	7	0	41
Wolf River (16)	17	21	23	24	63	69	0	1	1	6	2	10	1	2	17	68	1	326
Embarrass River (17)	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	3
Total	244	247	82	262	141	340	1	49	5	56	11	109	11	11	70	163	4	1,806

TABLE 3. Numbers and location of tagging and first and second recaptures of lake sturgeon recaptured only twice. Lake Winnebago and the Wolf River each include 6 areas.

Tagging Location	No. Recaptured, by Location								Total
	1st 2nd	Lake Winnebago Lake Winnebago	Lake Winnebago Wolf River	Wolf River Lake Winnebago	Wolf River Wolf River	Fox River Fox River	Lake Poygan Lake Winnebago	Lake Poygan Lake Poygan	
Lake Winnebago		58	3	11	8	0	0	0	80
Wolf River		17	5	6	15	0	1	0	44
Fox River		1	0	0	0	8	0	0	9
Lake Poygan		2	0	1	1	0	0	1	5
Total		78	8	18	24	8	1	1	138

TABLE 4. Location and date of tagging and recaptures of individual lake sturgeon recaptured 3 or 4 times.

Sex	Tagged		1st Recapture		2nd Recapture		3rd Recapture		4th Recapture		Years at Large*		
	Location (Area)	Date	Large*										
Unknown	Wolf (12)	Apr 54	Winnabago (2)	Sep 54	Winnabago (4)	May 79	Winnabago (6)	May 79	Winnabago (6)	May 79	Wolf (12)	Apr 64	25.0
Male	Wolf (12)	May 56	Wolf (12)	Apr 58	Wolf (12)	May 59	Wolf (12)	Apr 63	Wolf (12)	Apr 63	Wolf (12)	Apr 64	8.0
Male	Wolf (12)	May 56	Winnabago (1)	Apr 57	Winnabago (6)	Nov 60	Winnabago (6)	Feb 63	Winnabago (6)	Feb 63	Winnabago (6)	May 84	7.0
Unknown	Wolf (16)	Apr 78	Winnabago (3)	May 79	Wolf (16)	Apr 80	Winnabago (4)	May 84	Winnabago (4)	May 84	Winnabago (6)	May 82	6.0
Unknown	Wolf (16)	May 79	Winnabago (6)	May 79	Winnabago (6)	Feb 82	Winnabago (6)	May 82	Winnabago (6)	May 82	Winnabago (2)	Feb 67	3.0
Unknown	Winnabago (2)	Oct 55	Winnabago (1)	Jun 58	Winnabago (6)	May 64	Winnabago (2)	Feb 67	Winnabago (2)	Feb 67	Winnabago (6)	Feb 64	11.5
Female	Winnabago (2)	Aug 56	Winnabago (4)	Sep 57	Winnabago (2)	May 60	Winnabago (6)	Feb 64	Winnabago (6)	Feb 64	Winnabago (3)	Oct 61	7.5
Female	Winnabago (2)	Apr 60	Winnabago (4)	Oct 60	Winnabago (5)	Jun 61	Winnabago (3)	Oct 61	Winnabago (3)	Oct 61	Winnabago (1)	Feb 63	3.0
Unknown	Winnabago (3)	Jul 77	Fox (8)	Apr 80	Winnabago (1)	Aug 81	Winnabago (4)	Feb 82	Winnabago (4)	Feb 82	Winnabago (4)	Feb 82	4.5
Unknown	Winnabago (4)	May 57	Wolf (16)	Apr 60	Winnabago (6)	Apr 61	Winnabago (4)	Aug 64	Winnabago (4)	Aug 64	Winnabago (4)	Aug 64	7.0
Unknown	Winnabago (5)	Oct 55	Winnabago (2)	Aug 57	Winnabago (4)	Sep 57	Winnabago (2)	Jun 61	Winnabago (2)	Jun 61	Winnabago (4)	Aug 64	5.5
Unknown	Winnabago (5)	Apr 76	Winnabago (1)	Aug 76	Winnabago (6)	May 79	Winnabago (1)	Jul 84	Winnabago (1)	Jul 84	Winnabago (2)	Feb 66	8.0
Unknown	Winnabago (6)	Oct 58	Winnabago (2)	May 59	Winnabago (3)	May 61	Winnabago (2)	Feb 66	Winnabago (2)	Feb 66	Winnabago (2)	Feb 66	7.5
Male	Winnabago (6)	May 79	Wolf (16)	May 79	Winnabago (6)	May 82	Wolf (15)	Oct 83	Wolf (15)	Oct 83	Wolf (15)	Oct 83	4.5
Male	Winnabago (6)	Apr 81	Winnabago (6)	Jul 81	Wolf (16)	Apr 82	Wolf (16)	Apr 83	Wolf (16)	Apr 83	Wolf (16)	Apr 83	2.0
Female	Poygan (10)	Dec 56	Winnabago (3)	Oct 58	Winnabago (6)	Oct 60	Winnabago (6)	May 61	Winnabago (2)	May 61	Wolf (12)	Apr 78	21.5

*Rounded to the nearest 0.5 years.

was 3 years, and 17% of the captures occurred one year apart. If all tagged males were actually spawning every year but were not always captured, then the median value for the interval between captures might be greater than one year. However, in such a case, the mode would still be one, because mortality would reduce the number of tagged fish as the interval between captures increased, and because there would be more one-year intervals in which to capture fish than there would be longer intervals. Conversely, if sampling effort varied in some systematic fashion from year to year, the interval between captures might have a mode greater than one year even though all fish were spawning every year. While sampling effort (as measured by the number of fish tagged and recaptured) during spawning on the Fox and Wolf rivers varied substantially among years (Table 7), it was unclear how this variation influenced the interval between captures. During some periods, a year of low effort was preceded and followed by a year of higher effort (e.g., 1979-81 at area 16 of the Wolf), which might tend to produce a 2-year interval. During other periods, effort was roughly similar for several years (e.g., 1976-78 at area 12 of the Wolf), which could reveal a one-year interval. In some instances, a moderate number of fish were tagged each year for several years, but no recaptures were made until 3 years after tagging began (e.g., 1955-60 at area 16 of the Wolf); this is evidence for an interval of greater than one year.

Capture intervals for the 15 male lake sturgeon captured 3 or more times in the same river area during spawning also suggest that some males spawned every year but others did not (Table 8). Eight of the 15 fish were never captured at less than 2-year intervals, whereas the remaining 7 were captured during 2 successive years. Seven fish were captured only at regular intervals (1, 2, or 3 years).

Data were limited on the spawning periodicity of female lake sturgeon. Only 10 were observed more than once in a river during the spawning season, and one of those was observed twice in the same year (once in area 8 of the Fox and once in area 16 of the Wolf). The capture interval for most of the remaining 9 fish was 3 or 4 years, but one fish had a capture interval of only one year (Table 6). Thus, females probably spawned at greater intervals than males.

A longer interval between spawnings for females was consistent with the sex ratio of lake sturgeon in rivers during spawning. On the Wolf, Fox, and Embarrass rivers, nearly 9 out of 10 of the tagged and recaptured lake sturgeon that could be sexed were males (Table 9). If most of the spawning fish in the rivers came from the lakes and there were about equal numbers of males and females in the lakes

TABLE 5. Numbers of lake sturgeon captured more than once at a major spawning area during spring spawning. Only captures separated by at least one year are included.

First Capture Location (Area)	Location of Next Capture			Total
	Fox (8)	Wolf (12)	Wolf (16)	
Fox River (8)	39	2	0	41
Wolf River (12)	0	70	6	76
Wolf River (16)	1	16	69	86
Total	40	88	75	203

TABLE 6. Intervals (years) between captures for lake sturgeon captured more than once at a river spawning area during spring spawning.

Years Between Captures	No. Captured, by Sex		
	Males	Female	Total
1	34	1	35
2	63	0	63
3	42	4	46
4	30	2	32
5	15	1	16
6	5	0	5
7	6	0	6
8	1	1	2
9	1	0	1
>9	1 (21 years)	0	1
Total	198	9	207

TABLE 8. Years of recapture for male lake sturgeon tagged and subsequently recaptured more than once in the same river area during spawning.

Tagging and Recapture Location (Area)	Year Tagged	Year Recaptured			
		1st	2nd	3rd	4th
Wolf (12)	1956	1957	1958		
Wolf (12)	1956	1958	1960		
Wolf (12)	1956	1958	1959	1963	1964
Wolf (12)	1957	1959	1961		
Wolf (12)	1957	1962	1964		
Wolf (12)	1976	1979	1982		
Wolf (12)	1978	1979	1980		
Wolf (16)	1978	1980	1982		
Fox (8)	1976	1977	1981		
Fox (8)	1976	1978	1980		
Fox (8)	1976	1981	1983		
Fox (8)	1976	1980	1981		
Fox (8)	1977	1981	1983		
Fox (8)	1977	1980	1981		
Fox (8)	1977	1980	1981		

TABLE 7. Number of lake sturgeon tagged or recaptured each year during spawning at 3 river areas. If no fish were tagged or recaptured at an area during a year, then probably no effort was made to capture fish.

Year	Wolf River (Area 12)		Wolf River (Area 16)		Fox River (Area 8)	
	No. Tagged	No. Recaptured	No. Tagged	No. Recaptured	No. Tagged	No. Recaptured
1952-53	no tagging or recaptures					
1954	35	4	0	0	0	0
1955	70	1	31	0	0	0
1956	75	2	43	0	0	0
1957	6	0	55	0	0	0
1958	33	3	95	7	0	0
1959	67	5	3	0	0	0
1960	15	3	62	5	0	0
1961	2	2	19	3	0	0
1962	3	0	21	1	4	0
1963	9	2	5	1	0	0
1964	0	7	0	1	0	0
1965-74	no tagging or recaptures					
1975	8	1	56	1	36	0
1976	91	1	217	1	53	0
1977	75	2	192	1	67	2
1978	109	3	125	3	22	1
1979	236	14	262	33	0	0
1980	163	16	58	8	56	4
1981	40	2	263	33	71	17
1982	97	11	133	22	32	1
1983	121	27	129	34	63	24
1984	0	2	41	9	0	0
1985	0	1	0	0	0	0
Total	1,255	109	1,810	163	404	49

TABLE 9. Sex ratio of lake sturgeon captured in rivers. The number of captures includes tagging and all subsequent recaptures.

River (Season)	No. Captured, by Sex		Male:Female Ratio
	Male	Female	
Wolf (spring)	504	59	8.5:1
Wolf (fall)	13	1	13.0:1
Fox (spring)	106	11	9.6:1
Embarrass (spring)	6	0	—
Total	629	71	8.9:1

prior to spawning, then the sex ratio of spawners indicates that in any one year more males spawned than females, which would be the case if males had a shorter interval between spawning than females.

Wolf River Residency

At least a moderate number of lake sturgeon were present during the fall in areas 15 and 16 of the Wolf River (Table 10). These were the only river areas sampled outside the spring spawning period, except for some limited winter sampling in area 11 of the Wolf River during the 1950s. Some of the fish captured in the fall may have been permanent residents, but others had spent part of their lives in the lakes. One fish that was tagged in Lake Winnebago in the spring was recaptured in the Wolf River during the fall of the same year, and 21 fish captured from Lake Winnebago and 3 from Lake Poygan were captured over a year later in the Wolf River during the fall. Four fish that were tagged in the Wolf River during the fall were later recaptured in Lake Winnebago, one during the spring following tagging.

Most of the fish captured in the Wolf River during the spring spawning period were also not likely to be permanent residents, and many probably occupied the river only for the few days or weeks of spawning. Of 133 fish captured in the Wolf River during

spring spawning and then recaptured within 6 months, 132 were recaptured in Lake Winnebago and one was recaptured in Lake Winneconne. Of fish captured from the lakes within 6 months before spawning, 32 from Lake Winnebago and 4 from Lake Poygan were recaptured in the Wolf River during spawning. Two of these fish were tagged in Lake Winnebago, recaptured in the Wolf River during spawning, and then recaptured again back in Lake Winnebago, all within one month. Conversely, no fish were captured in the Wolf River in the spring and then recaptured there during the same year, and only one fish was captured in the Wolf River during the fall and then recaptured there the following spring. However, these last data are deceptive because the last year of spring sampling data for the Wolf River was 1983, at which point only 23 fish had been tagged there during the fall. Also, 20 fish that were captured during spring spawning in the Wolf River were recaptured there 1-2 years later during the fall. This finding, coupled with the similarity in sex ratios of lake sturgeon in the Wolf River during the spring and fall (Table 9), suggests that some lake sturgeon from the lakes move into the Wolf River during the fall and overwinter there before spawning during the spring and returning to the lakes.

Other Results

Recapture data provide a minimum estimate of the speed at which lake sturgeon can travel long distances. During the month of May in 1979, 2 lake sturgeon (mentioned above) were tagged in area 6 of Lake Winnebago, recaptured in area 16 of the Wolf River, and then recaptured again in Lake Winnebago (one in area 4 and the other in area 6). This represents a minimum of 285 miles traveled in a maximum of 31 days, for a minimum speed of 9.2 miles/day.

TABLE 10. Distribution of tagging and recaptures for lake sturgeon tagged in the Wolf River during the spring and fall and in Lakes Winnebago and Poygan during all seasons. Recaptures include multiple recaptures of the same fish.

Tagging Location (Season)	Total No. Tagged	Recapture Location (Season)				Total Recaptured
		Wolf (spring)	Wolf (fall)	Winnebago (all)	Poygan (all)	
Wolf River (spring)*	3,368	171	20	303	15	509
(fall)**	545	1	32	4	0	37
Lake Winnebago (all)	6,880	198	22	929	3	1,152
Lake Poygan (all)	1,960	11	2	43	37	93
Total	12,753	381	76	1,279	55	1,791

* Wolf (spring) tagging and recapture areas: 12, 13, 14, 15, 16.

** Wolf (fall) tagging and recapture areas: 15, 16.

Several lake sturgeon retained tags for long periods. One male was tagged during May 1956 in area 16 of the Wolf River and was recaptured 27.5 years later, during November 1983, in area 15 of the Wolf. Another fish was tagged in Lake Poygan during January 1956 and was recaptured 27 years later, during May 1983, in area 4 of Lake Winnebago. One female was tagged in Lake Poygan during December 1956 and then was recaptured 4 times during the next 21.5 years. Of the 1,632 tagged fish that were recaptured at least once, 4 were recaptured more than 25 years after tagging, another 5 were recaptured 20 to 25 years after tagging, and 5 more were recaptured 15 to 20 years after tagging.

Discussion

The patterns of adult lake sturgeon movement that emerge from our analyses of tag-recapture data are for the most part consistent with those patterns outlined by others who have studied the species in the Lake Winnebago system, as summarized in the introduction to this report. However, our analyses indicate that those patterns are not as rigid and invariable as these earlier studies concluded. Whereas most lake sturgeon have certain patterns of movement, usually at least a few individuals have different or variable movement patterns. Similar differences in the behavior of individuals were detected in a movement study of common carp (*Cyprinus carpio*) in the Lake Winnebago system (Otis and Weber 1982).

Our results support previous conclusions (Priegel and Wirth 1977) that lake sturgeon in Lake Winnebago move about extensively within the lake and do not appear to remain in any particular area for long periods of time. Our results also confirm that large numbers of lake sturgeon leave Lake Winnebago to spawn in the Wolf or Fox rivers during the spring (Probst and Cooper 1955; Priegel and Wirth 1977, 1978; Folz and Meyers 1985). However, tag-recapture data refute the idea that fish from the lakes are present in rivers only during spring spawning (Priegel and Wirth 1977). Although sampling effort in rivers was limited except during spring spawning, 28 fish that were captured in lakes were also captured during the fall in the Wolf River.

The tag-recapture data also support 2 previously reported patterns of movement that have important management implications: individual lake sturgeon tend to return to the same river area each time they spawn (Folz and Meyers 1985), and the lake sturgeon population in Lake Poygan has little contact with that

of Lake Winnebago except during spawning (Priegel and Wirth 1977, 1978). Taken together, these 2 movement patterns provide evidence that there may be separate stocks (populations) of lake sturgeon in Lake Poygan and in Lake Winnebago.

Whereas many lake sturgeon appear to display "homing" behavior during spawning, not all do; 10%-20% of spawners use different river spawning areas and sometimes different rivers altogether, over time. The failure of all sturgeon to home "perfectly" during spawning is likely to be adaptive, because if all sturgeon in a population always returned to spawn at the same site, elimination of that spawning area might eliminate the entire population.

The idea that Lakes Poygan and Winneconne have a stock of lake sturgeon separate from the Lake Winnebago stock was first proposed by Priegel and Wirth (1978), based on analyses of growth characteristics and population parameters (e.g., age structure, mortality) and a preliminary analysis of tag-recapture data from the 1950s and 1960s. They concluded that these analyses "have not shown any mixing to take place between the two populations" (p. 14). Our more detailed analyses of the now much increased tag-recapture data indicate that while the 2 populations are somewhat isolated from each other, some mixing occurs outside the spawning period. Fish tagged in Lake Poygan were more likely to be recaptured in Lake Winnebago than vice versa, which suggests that as Lake Poygan fish get older, some move into Lake Winnebago. This is consistent with the age distributions of speared lake sturgeon in the lakes; Lake Winnebago has a higher percentage of older fish (Probst and Cooper 1955; Priegel and Wirth 1975, 1978). However, differences in exploitation between Lake Poygan and Lake Winnebago may also contribute to the difference in age distributions (Priegel and Wirth 1978).

Prior to our analyses, male lake sturgeon in the Lake Winnebago system were thought to spawn every 1 or 2 years, and females were thought to spawn every 3 to 4 years (Folz and Meyers 1985) or every 4 to 6 years (Priegel and Wirth 1977). Long intervals between spawnings and more frequent spawning by males appear to be general characteristics of sturgeons in the genus *Acipenser* (Harkness and Dymond 1961, Dadswell 1979, Smith 1985). Our results are consistent with an annual or biennial spawning by males, although some males may not spawn at regular intervals. Our limited data suggest that most females spawn every 3 or 4 years, instead of every 4 to 6 years. To determine spawning intervals, we assumed that each lake sturgeon spawned during



PHOTO: APPLETON POST CRESCENT

A unique sport fishery takes place annually on Lake Winnebago from the second Saturday in February through 1 March, when lake sturgeon are harvested with spears through the ice. Darlene Homan of Neenah speared this 75-inch, 159-lb sturgeon in 1986.

each year in which it was captured in a spawning area of a river, an assumption that would not be valid if: (a) fish from a resident population in the spawning rivers are attracted to spawning fish (and are subsequently captured) but do not actually spawn, or (b) some fish from the lakes take part in the migration to the spawning areas without actually spawning. In South Carolina, mature Atlantic sturgeon (*Acipenser oxyrinchus*) sometimes participate in spawning migrations during years when they do not actually spawn (Smith 1985).

Sex ratio data also suggest that males spawn more frequently than females, but the 8.9:1 male:female ratio overestimates the difference in spawning frequencies between the sexes (Folz and Meyers 1985). Males are on the spawning grounds longer than females and thus have a greater chance of being captured, and even when both sexes are present, males are typically smaller and easier to catch (Priegel and Wirth 1977).

In the introduction to this report, we posed 2 questions about lake sturgeon movement in the Lake Winnebago system: (1) Do some adult lake sturgeon remain in the spawning rivers year-round? and (2) Do lake sturgeon from different lakes use different areas for spawning? Although our analyses shed light on both questions, existing tag-recapture data cannot conclusively answer either one.

For many years, it has been known that adult lake sturgeon occupy the Wolf River during the spring, but now it is clear that substantial numbers of adults also are present in at least parts of the river during the fall. Lacking data from summer and winter, we cannot be certain whether or not some of these fall-caught fish are permanent residents, but our results suggest that many are not. A number of the fall-caught fish had been marked outside the Wolf River, or were later recaptured outside the

river, and the sex ratio of the fall-caught fish was quite different from that of typical resident lake sturgeon populations (Harkness and Dymond 1961). In the Wolf River, several lake sturgeon were caught in or near the same spawning area during both the fall and spring, and the highly skewed sex ratio in the fall is essentially identical to that during spring spawning. The preponderance of males in catches from the Wolf River during the fall and spring contrasts with the preponderance of females in catches from Lake Winnebago during the winter (Probst and Cooper 1955); it seems logical that females would be more numerous than males in Lake Winnebago if many spawners, which are primarily males, had already moved into the spawning rivers. From these data, it seems likely that some fish move from the lakes into the upper areas of the Wolf River during the fall, overwinter there, spawn in the spring, and then return to the lakes. Some members of a spring-spawning shortnose sturgeon (*Acipenser brevirostrum*) population in New Brunswick move into spawning rivers in the fall and overwinter there (Dadswell 1979). Females are only slightly more common than males in catches from Lakes Poygan, Winneconne, and Butte des Morts during the winter (Probst and Cooper 1955), suggesting that spawners from these lakes may not leave as early for the spawning rivers as spawners from the Lake Winnebago population. However, 5 fish tagged in Lake Poygan in the fall or early winter were recaptured in area 11 of the Wolf River in mid- to late-winter.

The sex ratio data from the lakes are deceptive, however, and may have little to do with movement patterns of spawners. Sex ratio data from the lakes are from speared fish. Spearing selects for larger, older fish when they are available, and in both lakes, adult females typically live longer and grow larger than males (Probst and Cooper 1955). In Lake Winnebago, the lake sturgeon population is in good condition and spearers usually take a relatively high percentage of large, old fish (Folz and Meyers 1985), possibly contributing to the dominance of females in catches. Conversely, in Lakes Poygan, Winneconne, and Butte des Morts, large fish are relatively scarce, and spearers take a lower percentage of large, old fish (Priegel and Wirth 1978), possibly accounting for the lower percentage of females in the catches from these lakes.

Although overlap occurs, Lake Poygan lake sturgeon tend to spawn in different areas in the Wolf River than Lake Winnebago lake sturgeon. Different spawning areas should help maintain isolation between the populations in the 2 lakes. Most lake

sturgeon caught in both the Wolf River and in Lake Winnebago were captured in area 16 of the Wolf River during the spring, with a much smaller number caught in area 12. Conversely, most lake sturgeon caught in both Lake Poygan and the Wolf River were captured in area 12 of the Wolf River during the spring. Only fish tagged in Lake Winnebago or the Wolf River have been recaptured in the Fox or Embarrass rivers.

A major stumbling block in using the tag-recapture data to evaluate patterns of lake sturgeon movement has been the lack of information on the type and relative amount of sampling effort within each area and time period. Because the data we used came from sampling that often was not designed to examine lake sturgeon movement and sometimes did not even target lake sturgeon, we were often uncertain whether low catches of lake sturgeon from an area or time period reflected a lack of adequate sampling or a lack of lake sturgeon. Thus the overall results of our analyses may be biased in a variety of ways having little to do with true patterns of lake sturgeon movement. For most of this report, we have assumed that sampling effort was roughly proportional to the total number of lake sturgeon captured in each area. This may not be a valid assumption, but if it is, then sampling effort was greater in Lake Winnebago than in any other lake in the study area and greater in the Wolf River than in any other river. Therefore, the fact that most taggings and recaptures occurred only in Lake Winnebago and the Wolf River does not necessarily mean that most lake sturgeon in the Lake Winnebago system move only within or between these 2 bodies of water. Lake sturgeon occupancy and use of Lake Butte des Morts and Winneconne are probably much greater than indicated by the tag-recapture data. Clearly, despite 34 years of tag-recapture data, more remains to be learned about lake sturgeon movement patterns in the Lake Winnebago system.

Management Implications

The results of our analyses have 3 major implications for management. First, although they are not as completely isolated from each other as previously believed, lake sturgeon from Lake Poygan and Lake Winnebago appear to be part of separate populations and should continue to be managed separately. Second, lake sturgeon tend to use the same areas each time they spawn. In order to maintain healthy populations, these areas need to be protected from

alteration or degradation (see also Folz and Meyers 1985). Third, a population of adult lake sturgeon may reside in the Wolf River all or at least most of the year (October to May). These fish may require a different management strategy than fish that spend most of their time in the lakes.

The lake sturgeon tag-recapture program has provided much insight into the patterns of movement of adult lake sturgeon in the Lake Winnebago system. This program will increase in value if its focus and objectives change. The questions that remain about lake sturgeon movement patterns require a sampling scheme designed specifically to look at movement. Tag-recapture data from studies with other objectives, such as estimating spearing exploitation, are unlikely to effectively address these questions and may in fact yield erroneous answers. Given the large size and complexity of the Lake Winnebago system, future tag-recapture efforts must be directed at specific questions that involve tractable sampling schemes. Two sets of questions that deserve study are:

1. Are adult lake sturgeon present in the Wolf River other than during spring and fall? Are they present in the Fox and Embarrass rivers other than during spring? If so, are these fish long-term residents or recent migrants from the lakes?
2. Where do lake sturgeon from Lake Winneconne and Lake Butte des Morts spawn and how much do they mix with the populations in Lakes Poygan and Winnebago?

Ideally, each of these sets of questions would be addressed through standardized sampling of all areas of the system during all seasons, but realistically this is not possible. Clearly, however, more sampling must take place outside of Lakes Winnebago and Poygan and the Wolf and Fox rivers, and more sampling must take place in rivers during non-spawning periods. Since 1985, fisheries biologists have begun to sample rivers in the Lake Winnebago system outside of the spawning period (Dan Folz, Wis. Dep. Nat. Resour. retired, pers. comm.), but their data are not yet available. Equally important is the need for some attempt to quantify tagging and recapture effort, in order to account for variation in number of fish tagged or recaptured due to variation in that effort. If possible, a standard amount of comparable

sampling effort should be expended in each area and time period. Whereas sampling techniques will not be directly comparable between lakes and rivers, comparable techniques can be used within lakes and within rivers. This means that if electroshocking is the only effective way to catch adult lake sturgeon in rivers during non-spawning periods, then electroshocking should also be attempted during spawning periods, in addition to standardized dip-netting. Tag-recapture data collected during sampling that is not part of the movement study should not be ignored but should be analyzed and interpreted separately.

Radio-tagging of adult lake sturgeon will help answer both sets of questions, but should not be used as a substitute for tag-recapture efforts. Radio-tagging can reveal where fish are on a day-to-day basis, including periods when capture of lake sturgeon is difficult (e.g., winter in rivers). Radio-tagging also provides much better estimates of distance traveled and speed of travel, and it is especially good for identifying short-term movement patterns (e.g., Hay-Chmielewski 1987). However, the number of fish that can be radio-tagged or tracked at one time is typically small, and the behavior of radio-tagged fish may not be representative of the population as a whole. Also, radio tags usually last less than 2 years, so they are not particularly useful for studying movement patterns that occur over a longer time, such as the homing behavior of spawning female lake sturgeon. Conversely, in a tag-recapture program, many lake sturgeon can be tagged, often during a short period (e.g., spring spawning), and some of the tags may remain on lake sturgeon for many years. Thus, radio-tagging and tag-recapture programs are complimentary to each other. Since 1985, fisheries biologists have used both approaches together in a coordinated fashion to monitor lake sturgeon movement in the Lake Winnebago system (Dan Folz, pers. comm.), and they should continue this in the future.

Finally, more needs to be known about the degree of isolation between Lake Poygan and Lake Winnebago lake sturgeon. Tag-recapture data will continue to be valuable in this regard, but we feel that other approaches, such as quantitative comparisons of morphological or genetic differences between populations, are also necessary.

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