Seasonal movements of lake sturgeon in Lake of the Woods and the Rainy River, Ontario

J.A. Rusak and T. Mosindy

Abstract: Lake sturgeon (*Acipenser fulvescens*) inhabiting the southern portion of Lake of the Woods and the Rainy River, a north-temperate watershed straddling the Canada – United States border, were studied to test hypotheses concerning seasonal movement patterns, including spawning migrations, and habitat use. We implanted radio transmitters into 26 fish and monitored seasonal movements during 3 consecutive years. Data indicated the existence of two discrete populations of sturgeon in this watershed, differentiated by seasonal habitat use, movement patterns and rates, and timing of spawning. The "lake" population, a designation suggested by a consistent preference for lentic winter habitat, appeared to spawn and initiate extensive spring and summer movements later than the "river" population, which consistently inhabited the river during the winter months. Overall, movement rates were significantly greater in the spring and summer months than at other times of the year and decreased with water temperature. General preferences exhibited by lake sturgeon for certain habitat types at different times of the year appeared to be linked to foraging behaviour. The results suggest that population differentiation may be prevalent for this species inhabiting large lake–river systems, given some diversity in habitat structure and spawning cues. In management efforts, this potential should be taken into consideration and reflected.

Résumé : Les déplacements de l'Esturgeon jaune, *Acipenser fulvescens*, ont été suivis dans la portion sud du lac Lake of the Woods et dans la rivière Rainy, un bassin hydrographique tempéré nord qui chevauche la frontière Canada – États-Unis, afin d'éprouver les hypothèses sur les déplacements saisonniers, notamment les migrations de fraye et l'utilisation de l'habitat. Nous avons muni 26 poissons d'émetteurs radio et avons enregistré leurs déplacements au cours de 3 années consécutives. Les données ont révélé l'existence de deux populations distinctes d'esturgeons dans le bassin, différentes par leur utilisation saisonnière de l'habitat, par leurs itinéraires et vitesses de déplacement et par le moment de leur fraye. La population « de lac », une appellation suggérée par la préférence marquée de ces poissons pour les milieux lénitiques en hiver, avait une fraye plus hâtive et se livrait à des déplacements importants au printemps et en été plus tard que la population dite « de rivière » qui restait dans la rivière au cours de mois d'hiver. Dans l'ensemble, la fréquence des déplacements était significativement plus élevée au cours des mois de printemps et d'été qu'en tout autre temps de l'année et diminuait à mesure que la température de l'eau baissait. Les préférences globales de l'Esturgeon jaune pour certains types d'habitats à différents moments de l'année semblent reliées au comportement de recherche de nourriture des poissons. Les résultats semblent indiquer que la différenciation démographique peut être très importante chez cette espèce des grands systèmes lac–rivière, étant donné la diversité dans la structure de l'habitat et les facteurs déclencheurs de la fraye. Les programmes d'aménagement doivent tenir compte de cette possibilité.
[Traduit par la Rédaction]

Introduction

Long-term seasonal movement patterns of lake sturgeon (*Acipenser fulvescens*) are largely unknown, especially in lake environments (Scott and Crossman 1973). Most studies of this species have been based on short-term observations (Bassett 1982; Hay-Chmielewski 1987; Thuelmer 1988), while multiple-season research has been limited to North American riverine species, such as the shortnose sturgeon (*A. brevirostrum*), white sturgeon (*A. transmontanus*), and shovelnose sturgeon (*Scaphirhynchus platorynchus*) (Buckley and Kynard 1985; Dadswell 1979; Hall et al. 1991; McCleave et al. 1977; Haynes and Gray 1981; Hurley et al. 1987). Sturgeon occurring in contiguous lake and river systems are thought to use lakes throughout most of the year and rivers primarily for spawning and occasional summer feeding (Harkness and Dymond 1961; Scott and Crossman 1973; Priegel and Wirth 1978). In lakes, movement patterns have been reported to be both restricted (Harkness and Dymond 1961; Bassett 1982) and far-ranging (Priegel and Wirth 1971; Hay-Chmielewski 1987; Auer 1993), with or without some semblance to a "home range." In larger rivers, without links to lakes, differentiation between spawning and seasonal patterns becomes more difficult, but shortnose sturgeon appear to exhibit definite seasonal patterns of movement outside of spawning migrations. (Dadswell 1979; Buckley and Kynard 1985; Hall et al. 1991).

Given this variation, managers require knowledge of seasonal movements and habitat use in order to protect or improve areas critical for survival and reproduction. This information can also be of benefit in attempts to regulate the

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harvest of specific populations, especially in larger water bodies. In this study, we document the seasonal movements, spawning migrations, and macrohabitat use of lake sturgeon that have access to both Lake of the Woods and the Rainy River. The extent and variation of seasonal movements among lake sturgeon were also investigated using radiotelemetry data from 3 consecutive years of monitoring.

Materials and methods

Study area

Both Lake of the Woods and the Rainy River are part of the Winnipeg–Nelson river system that flows northwards into Hudson Bay. Lake of the Woods is situated on the Canada – United States border, where the state of Minnesota and provinces of Ontario and Manitoba meet (Fig. 1). Sturgeon are largely restricted to the southern half of Lake of the Woods, concentrated in the Big Traverse basin, and the Rainy River. The lake covers about 385 000 ha, two-thirds of which lies in Canada. The Rainy River enters at the extreme southeast corner of Lake of the Woods and is the largest tributary, accounting for over 70% of the annual inflow to the lake. The river flows approximately 140 km between Rainy Lake and Lake of the Woods through forested and marginal agricultural land that is used mainly as pasture for livestock. The river is controlled at the outflow from Rainy Lake by a hydroelectric dam built in 1909 to power paper mills in Fort Frances and International Falls. Prior to the dam's construction, a waterfall provided a natural barrier to upstream fish migration. Major tributaries flowing into the Rainy River include the Big Fork, Little Fork, Black, and Rapid rivers on the Minnesota side and the Pinewood, Sturgeon, and La Vallee rivers in Ontario.

While most of this area lies on Precambrian Shield, the southern portion of Lake of the Woods and the Rainy River and its tributaries are underlain by old lake sediments deposited by postglacial Lake Agassiz (Schwartz and Thiel 1963). As a result, the Big Traverse basin is shallower, more turbid, and considerably more productive, on average, than most of the lake, with a calculated morphoedaphic index (Ryder 1965) of 18.6, mean depth of 7.4 m, and total dissolved solids concentration of 138 mg/L. The Rainy River ranges in size from a mean depth of 1.9 m and mean width of 245 m in its upper reaches to a mean depth of 5.4 m and mean width of 350 m in its lower reaches. River water is brown-stained with humics (i.e., mean colour = 60 Pt units), with a mean total suspended solids concentration of 5.6 mg/L and a mean total phosphorus concentration of 0.023 mg/L (Beak Consultants Limited 1990). Lake sturgeon commercial fisheries with a total harvest quota of 5820 kg/year were located on both the lake and river until 1995. Following reallocation, a sport fishery and a native subsistence fishery for lake sturgeon remain on the Rainy River, with a combined annual harvest estimate of 2000 kg.

Sampling protocol

We captured lake sturgeon over three sampling seasons (April–June in 1987–1989), using 203-, 254-, and 305-mm mesh (stretched) multifilament gill nets (90.0 × 3 m). Sites at Long Sault Rapids, Burton Island, and Four Mile Bay were fished each year (Fig. 1). The majority of fish were tagged at the latter location. Actual netting sites varied from year to year, since nets were set to maximize the number of fish caught. All sturgeon were sampled for total and fork lengths (mm) and mass (kg). Fish were tagged with small yellow oval disc tags that were fastened with monofilament fishing line just anterior to the dorsal fin in 1987 and posterior to this fin in 1988 and 1989. In 1989, the dorsal fin of sampled sturgeon was also notched. Alternate pectoral fin rays were taken from each fish in successive sampling years for age determination (Wilson 1987). Ageing of dried and sectioned fin rays was done microscopically (compound microscope, transmitted light and 40× magnification) by counting the number of white bands (corresponding to winter growth). This procedure for age estimation has recently been validated for both lake (Rossiter et al. 1995) and white sturgeon (Brennan and Caillet 1991). Fin rays were aged by two individuals and, when ages differed, were re-aged by the senior reader, who assigned the final value. Potential candidates for radio-transmitter implants were examined internally in 1988 and 1989 to determine sex and state of maturity according to macroscopic criteria modified from those of Guénette et al. (1992) for females and Huff (1975) for males. Assigning maturity solely on the basis of macroscopic characters can be difficult. Both male and female adult sturgeon do not spawn every year and instead progress through various stages of a maturation cycle. We therefore adopted conservative criteria for assigning maturity from our macroscopic examinations. Females were judged to be sexually mature when large (4+ mm) brown eggs were visible in the ovaries. Only males with white testes were considered to be sexually mature.

We surgically implanted radio transmitters fitted with trailing external whip antennae (30–45 cm long) into the body cavities of 18 fish in 1988 (Advanced Telemetry Systems (ATS) Model No. 8, 3 years' life expectancy, 72.5 g) and 8 fish in 1989 (Lotek Model No. FRT-2, 1.5 years' life expectancy, 30 g). Transmitters were implanted ventrally through a 10 cm long off-midline incision in the abdominal cavity. The antenna was externalized, approximately 10 cm behind the incision, using a shielded-needle technique (Ross 1982). Incisions were closed with absorbable nylon suture and there was no postoperative injection of antibiotics. During surgery, unanaesthetized fish were suspended, dorsal side down, in an inclined hammock that was positioned in a water-filled cattle trough. The fish's head was fully immersed in water, allowing the fish to breathe throughout the procedure. Radio-tagged fish were selected to ensure representation of spawners and nonspawners of both sexes from all three capture areas. All fish were released at the site of capture.

Locations of radio-tagged fish were "fixed" at least twice a week throughout the spring, weekly during the summer, twice a month in the fall, and monthly in the winter from May 1988 until October 1990. We flew over the study area in an Ontario Ministry of Natural Resources (OMNR) de Havilland Turbo Beaver aircraft equipped with ATS loop antennas mounted on each wing. Signals were received (ATS 2 MHz or a programmable Lotek SRX-400 scanning receiver) within a range of 5–10 km, depending on fish depth and ice cover. Although the aircraft usually cruised at an altitude of 300–455 m and at an average airspeed of approximately 195 km/h during tracking, both altitude and airspeed were often lowered to help pinpoint individual fish. An opportunity arose early in the study to quantify the precision of the telemetry data when one of the signals became stationary (we believe that the fish was harvested and the transmitter discarded, as our efforts to retrieve the fish were unsuccessful). Without this prior knowledge, the equivalent of blind trials, at normal cruising airspeed and altitude, were conducted in the river on the following three flights. The mean distance between successive weekly ice-free locations was 0.43 km (SD = 0.32 km; n = 3). Given our objective of quantifying large-scale movement patterns, this type of precision was more than adequate. Blind trials were not performed during the period of ice cover, but neither signal strength nor our ability to locate fish appeared to be impaired during the winter. Each aerial monitoring event continued until all fish had been located or the entire study area had been covered, barring problems with weather or fuel. With a maximum depth of 11 m in the study area, which was well within the reception range of the telemetry equipment, the occasions on which all fish were not located were few.

Daily river water temperatures were recorded by water treatment plant staff for the Town of Rainy River. Daily flow data from a station at Manitou Rapids were provided by the Canada Water Survey Branch.

Fig. 1. The study area, including the southern half of Lake of the Woods and all of the Rainy River.

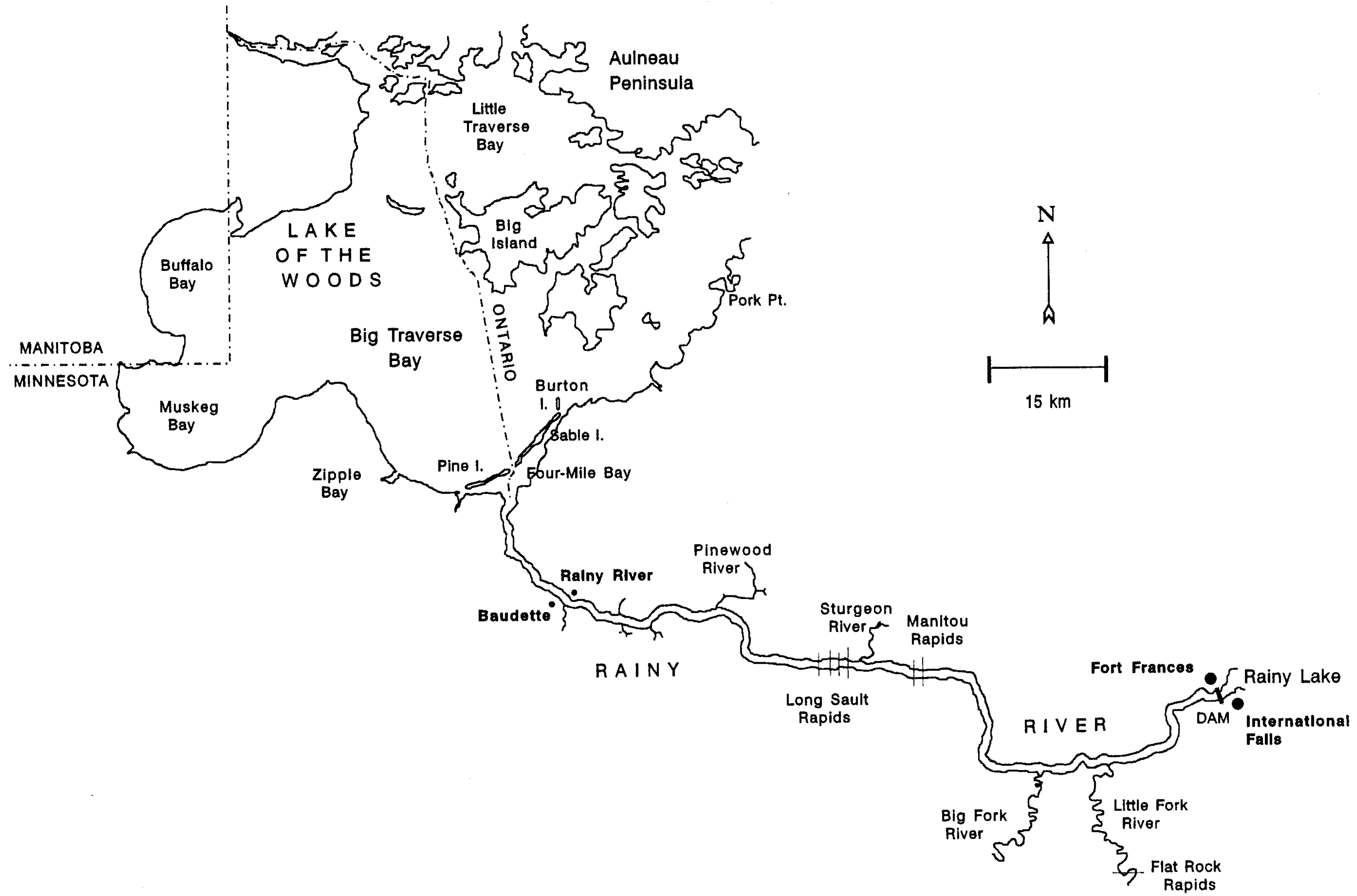


Table 1. Description of radio-tagged lake sturgeon whose seasonal and spawning movements in Lake of the Woods and the Rainy River, Ontario, were monitored.

Radio-tag frequency (MHz)	Fork length (mm)	Mass (kg)	Age (yr)	Sex	Gonad condition	Tagging date	Tagging location
49.020	1201	13.00	26	M	White testes	88-05-04	Four Mile Bay
49.051	1295	20.50	26	F	Brown eggs	88-05-04	Four Mile Bay
49.070	915	10.75	16	M	White testes	88-05-03	Four Mile Bay
49.089	1120	13.00	20	M	Yellow testes	88-06-01	Burton Island
49.109	1229	16.80	31	M	White testes	88-05-03	Four Mile Bay
49.129	1053	12.50	17	M	White testes	88-05-05	Four Mile Bay
49.150	1190	16.50	26	M	White testes	88-05-06	Four Mile Bay
49.170	1279	17.35	37	M	Yellow testes	88-05-06	Four Mile Bay
49.190	1104	14.50	19	M	White testes	88-05-03	Four Mile Bay
49.211	1164	12.00	29	F	Yellow eggs	88-05-17	Four Mile Bay
49.229	1279	17.70	22	M	White testes	88-05-07	Four Mile Bay
49.269	1163	16.84	30	F	Yellow eggs	88-05-06	Four Mile Bay
49.290	1372	27.50	32	F	Brown eggs	88-05-07	Four Mile Bay
49.307	1256	15.50	26	F	Yellow eggs	88-05-03	Four Mile Bay
49.369	1180	12.00	22	F	Yellow eggs	88-05-18	Long Sault Rapids
49.539	1330	21.55	32	F	Yellow eggs	88-05-04	Four Mile Bay
49.590	1158	14.50	22	M	Yellow testes	88-06-10	Burton Island
49.609	1301	18.50	32	F	Yellow eggs	88-05-05	Four Mile Bay
49.625	1128	12.75	19	M	Ripe white testes	89-05-20	Long Sault Rapids
49.645	1201	16.50	24	M	Yellow testes	89-06-15	Burton Island
49.665	1038	11.25	17	M	White testes	89-05-24	Burton Island
49.685	1156	14.00	21	M	Ripe white testes	89-05-17	Long Sault Rapids
49.705	1076	13.00	18	M	White testes	89-05-11	Four Mile Bay
49.725	1043	7.25	15	M	Ripe white testes	89-05-17	Long Sault Rapids
49.745	1221	14.00	20	M	Yellow testes	89-06-01	Burton Island
49.765	1134	11.75	23	M	White testes	89-05-16	Four Mile Bay

Note: Fish were released at the point of capture.

Analytical protocol

We used radiotelemetry data to interpret seasonal and spawning movements of tagged sturgeon and to determine if a suspected population segregation (Mosindy and Rusak 1991) was reflected in life-history attributes related to seasonal movement patterns or rates. All statistical analyses were conducted with SPSS/PC+4.0 (Norušis 1990).

Seasonal movements and spawning migrations

Seasons were loosely defined according to river water temperature trends. These corresponded to a spring increase in river water temperatures following the onset of river-ice breakup (April 5 – June 21) until the upper temperature limit for spawning (15°C; Scott and Crossman 1973) was reached; a summer (June 22 – August 15) warming; a fall (August 16 – October 31) cooling; and a relatively stable, cold winter period (November 1 – April 4). We mapped telemetry fixes to identify annual movement patterns, spawning migrations, and both spawning and nonspawning habitat use. We also attempted to determine if temperature and discharge were important factors in initiating different types of movement by comparing the onset of a particular movement pattern with observed cycles of water temperatures and river flows.

Movement rates

Year-round nonspawning movement rates were calculated as the $\log_{10}$-transformed linear distance (km) between successive fixes divided by the number of elapsed days. We tested whether differences in movement rates could be explained by season, sex, or winter habitat use (three-way non-orthogonal ANOVA). Differences among seasonal means were tested with Scheffé's multiple comparison test. Differences in movement rates were then examined within each individual season, by sex and winter habitat use, with one-way ANOVAs. Data on spawning migrations were excluded from all analyses of seasonal movement data.

Results

In total, 1593 fixes were collected on 18 lake sturgeon radio-tagged in May 1988 and 8 radio-tagged in May 1989. Fish from both years were tracked until the beginning of October 1990. With the exception of the single transmitter that became stationary after the first summer and three other transmitters, with 1.5 years' life expectancy, that failed in the summer of 1990, all signals were received until the end of the study. On average, radio-tagged fish had a fork length of 1177.5 mm (range 915–1372 mm), mass of 15.06 kg (range 7.25–27.5 kg), and age of 23.9 years (range 15–37 years). Eighteen fish were male and 8 were female (Table 1). Five male and six female sturgeon were immature. Mosindy and Rusak (1991) reported a mean age at maturity of 16.8 years for males and 25.8 years for females, based on a combined sample ($n \approx 1000$ fish) of commercial and experimental catches. Detailed population statistics and information on spawning periodicity are also available in that paper.

Fig. 2. Lake sturgeon overwintering areas during 1988–1990 in Lake of the Woods and the Rainy River. Open triangles represent locations of individual lake fish, while shaded squares represent those of river fish. Ellipses and rectangles indicate preferred areas of winter habitat.

Seasonal movements

Winter

Telemetry data indicated an apparent split in population structure, primarily differentiated according to winter habitat use. Radio-tagged sturgeon demonstrated consistent preferences for specific areas of the lake and river during winter tracking (Fig. 2). Thirteen fish spent the winter months in the lake, while 12 remained in the river. Sturgeon tagged in May 1988 displayed complete macrohabitat (lake or river) fidelity during the two consecutive winters of monitoring and returned to the same areas in the fall of 1990. However, individual fish did not always maintain overwintering-site fidelity (i.e., use of the same overwintering area) within the lake and river habitats over the course of the study. Fish overwintering in the lake were consistently more likely to occupy and keep the same site (62% between years and 73% within a given year) than fish using the river (44% between years and 62% within a given year).

"River" fish remained exclusively in the Rainy River, preferring certain stretches between Long Sault Rapids and Lake of the Woods (Fig. 2). The mean distance moved between tracking events by river fish during the winter was 1.7 km (all three winters of data combined; SD = 2.99 km, n = 153). The mean area of movement for individual fish (i.e., winter home range) was confined to a river distance of 5.2 km (1988 and 1989 winters; SD = 6.45 km, n = 22). No radio-tagged fish were found above Long Sault Rapids. These rapids are the first encountered as one moves upstream and essentially divide the river in half. Midchannel water depths (6–11 m) and flow conditions are similar along most of the river downstream of Long Sault Rapids.

"Lake" fish were only found in the lake during the winter months, concentrating in specific areas of the Big Traverse basin (Fig. 2), in fairly close proximity to the Rainy River mouth. These areas were characterized by a soft substrate (i.e., sand and (or) mud) at water depths greater than 7.0 m and off mainland or island shorelines. Water depths in this area do not exceed 11.5 m. The mean distance moved by lake fish, between fixes, during the winter was 2.8 km (all three winters of data combined; SD = 3.14 km, n = 155). Winter home ranges of individual fish were confined to areas with

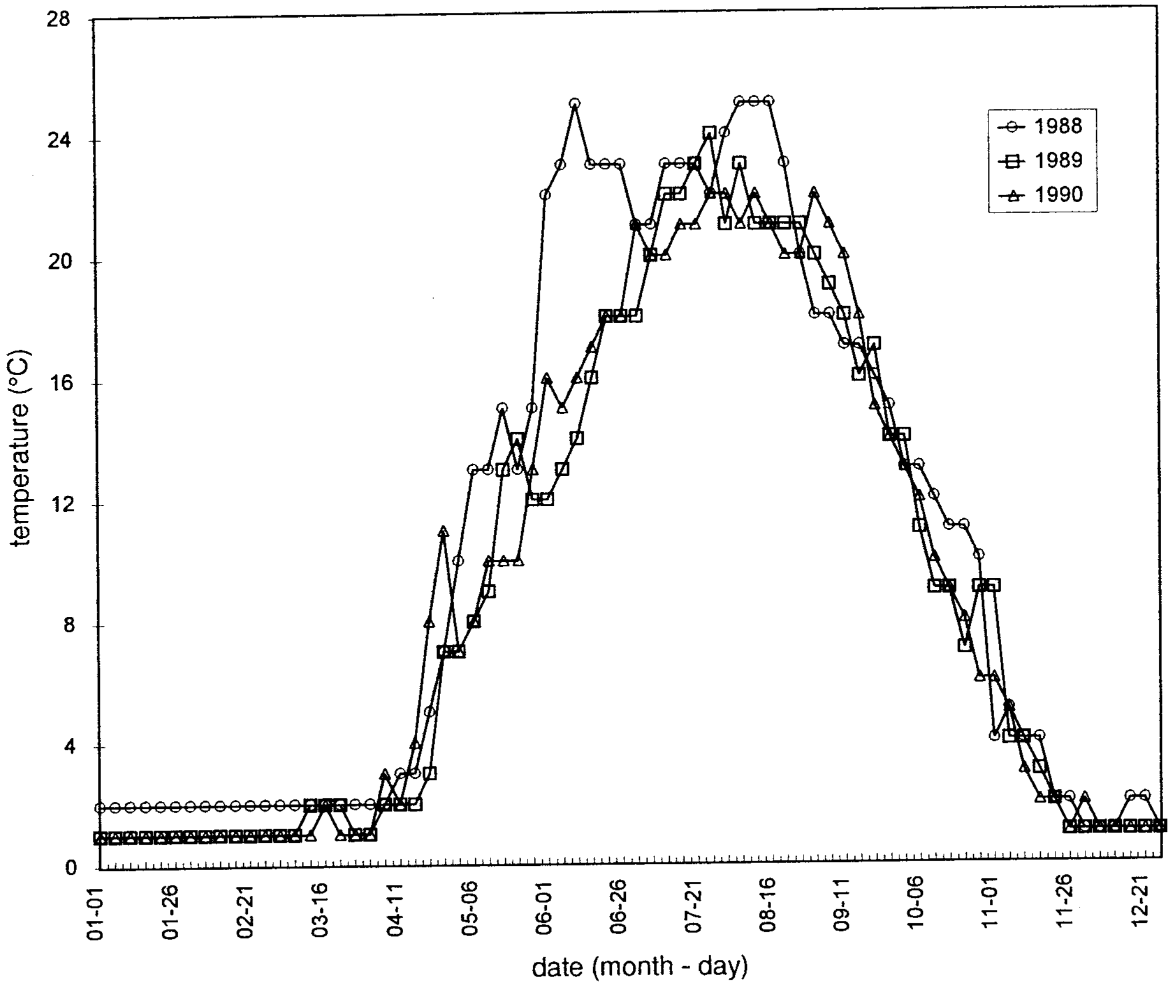


Fig. 3. River surface temperatures at the town of Rainy River during 1988–1990. Temperatures represent a maximum value for a given day.

Table 2. Day of entry to the lake and return to the river, and the corresponding flow and temperature on that day, for nonspawning lake sturgeon overwintering in the river.

	1988		1989		1990		All years	
	Entry	Return	Entry	Return	Entry	Return	Entry	Return
Day of the year*	136.2 (17.5)	232.2 (46.1)	136.3 (19.6)	215.9 (32.1)	123.3 (18.9)	203.1 (34.1)	131.8 (19.3)	214.6 (35.7)
Date	17 May 1988	20 Aug. 1988	16 May 1989	4 Aug. 1989	3 May 1990	22 July 1990		
Flow*	163.8 (16.8)	387.4 (415.1)	676.2 (106.1)	560.1 (295.1)	254.6 (132.6)	550.9 (304.0)	431.7 (254.9)	523.7 (316.4)
Temperature*	15.8 (5.2)	20.2 (6.1)	10.3 (4.3)	19.8 (4.6)	11.0 (4.4)	19.7 (1.6)	11.6 (4.8)	19.8 (4.0)
n	5		12		9		26	

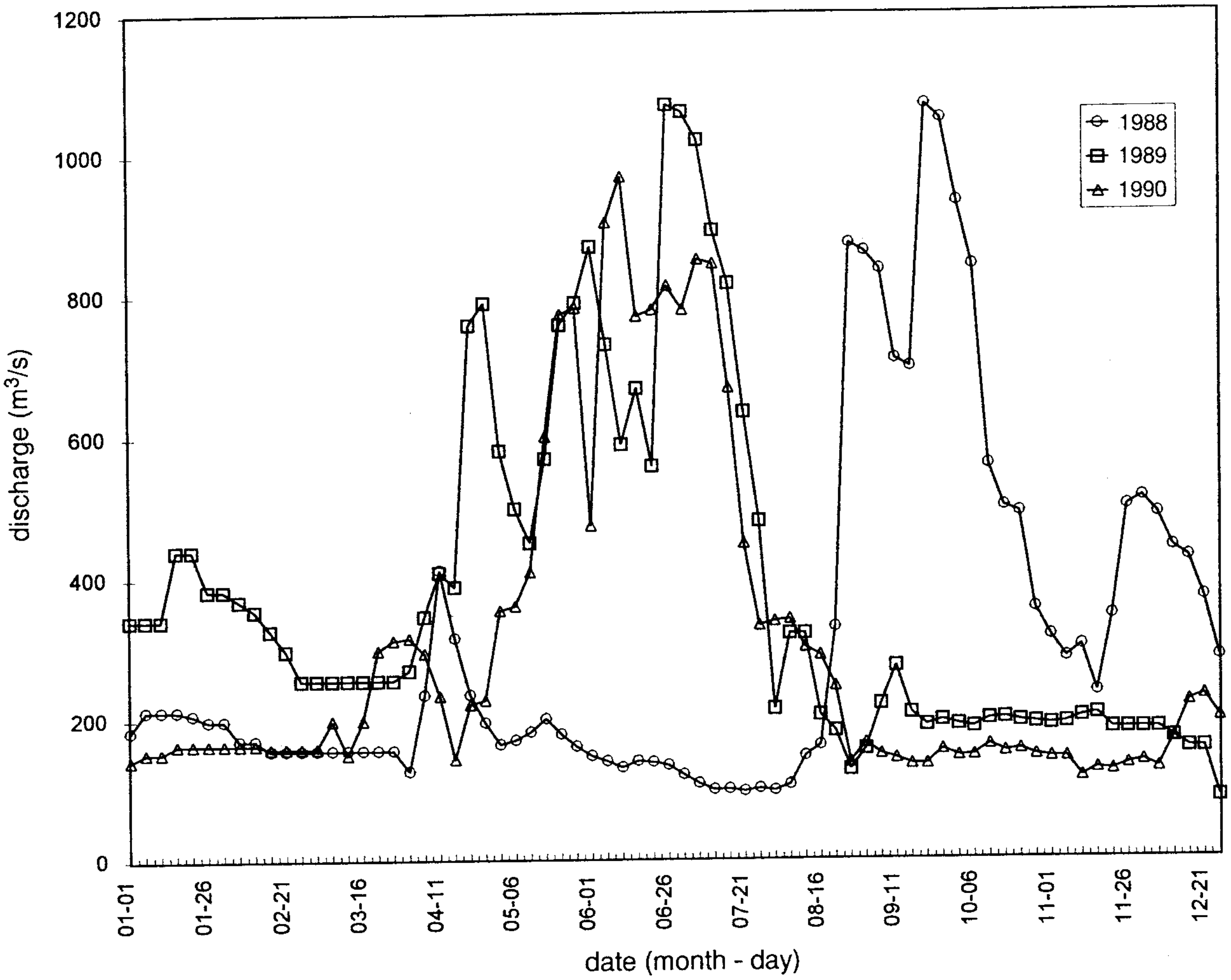
*Values are given as the mean, with the standard deviation in parentheses.

a mean diameter of approximately 5–6 km ($\bar{x}$ = 5.2 km, SD = 4.6 km; $\bar{y}$ = 5.9 km, SD =5.0 km; n = 20). It was noted that the locations on the lake with the highest densities of radio-tagged fish were those associated with increased water movement (e.g., in channels, around peninsulas, at river mouths).

Spring and summer

Extensive movements of nonspawning fish began early in the spring. River fish moved out into the lake at the start of May and lake fish began moving around the lake by mid-May. Past monitoring had indicated that the lake warmed up later and more gradually than the river. The mean annual date of entry to the lake by river fish varied from May 3 to 16 during the three spring seasons monitored (Table 2). In an effort to identify cues that might account for this variation, we looked for correspondence between the time at which river fish entered the lake and returned to the river and the patterns of river flows and temperatures (Figs. 3 and 4). The cue for spring movement by river fish into the lake was increases in both temperature and water flow. The return of these fish to

Fig. 4. River discharge rates at Manitou Rapids, Rainy River, during 1988–1990. Discharge rates represent a mean value for a given day of the week.



the river coincided with the occurrence of summer river temperature maxima in all 3 years (Fig. 3).

Although distances and directions travelled by radio-tagged fish varied, several distinct movement patterns emerged as the spring to summer warming trend continued (Figs. 5 and 6). Fish movements were primarily confined to the Big Traverse basin, including Muskeg and Buffalo bays. However, one fish was tracked northwards into Little Traverse Bay and another small group moved along the mainland shoreline as far east as Pork Point. Movement appeared to be oriented along mainland or island shorelines, away from the central portions of the Big Traverse basin.

The group of fish that overwintered in the lake entered the Rainy River only on their spawning migration, with the exception of one fish that was observed for a short period of time during the spring and summer in the lower reaches of the Rainy River (Fig. 5). All but one of the river fish moved out into the lake during this period. This individual remained in the river for the entire 3 years of monitoring. Most fish that overwintered in the river had returned to the lower reaches of the Rainy River and Four Mile Bay, at the river mouth, by early August (Table 2). Many lake fish tended to congregate at the river mouth at this time.

Fall

No long-range movements of river fish were observed during this period (Fig. 7). Only a few fish made extensive movements in August, following basinwide patterns similar to those observed during the spring and summer. Most lake and river sturgeon had returned to their overwintering areas by the end of October, when water temperatures ranged between 4 and 9°C and river flows were at their lowest for the year (Figs. 3 and 4).

Movement rates

We tested whether differences in movement rates existed among seasons and, if so, whether these differences were related to winter habitat use (i.e., river or lake overwintering) or to the sex of individual fish. Significant differences in movement rates among seasons were found ($p < 0.0001$) when all data were pooled. There were no overall differences in movement rates for either sex or winter habitat preferences, and no significant two- or three-way interactions that might confound seasonal differences (three-way ANOVA of movement rates by season, sex, and habitat). An examination of where the seasonal differences occurred showed that only spring and summer were not significantly different (Scheffé's

Fig. 5. Spring movement patterns of lake sturgeon during 1988–1990 in Lake of the Woods and the Rainy River. Open triangles and broken lines represent individual locations and generalized movements of lake fish. Shaded squares and solid lines indicate locations and movements of river fish.

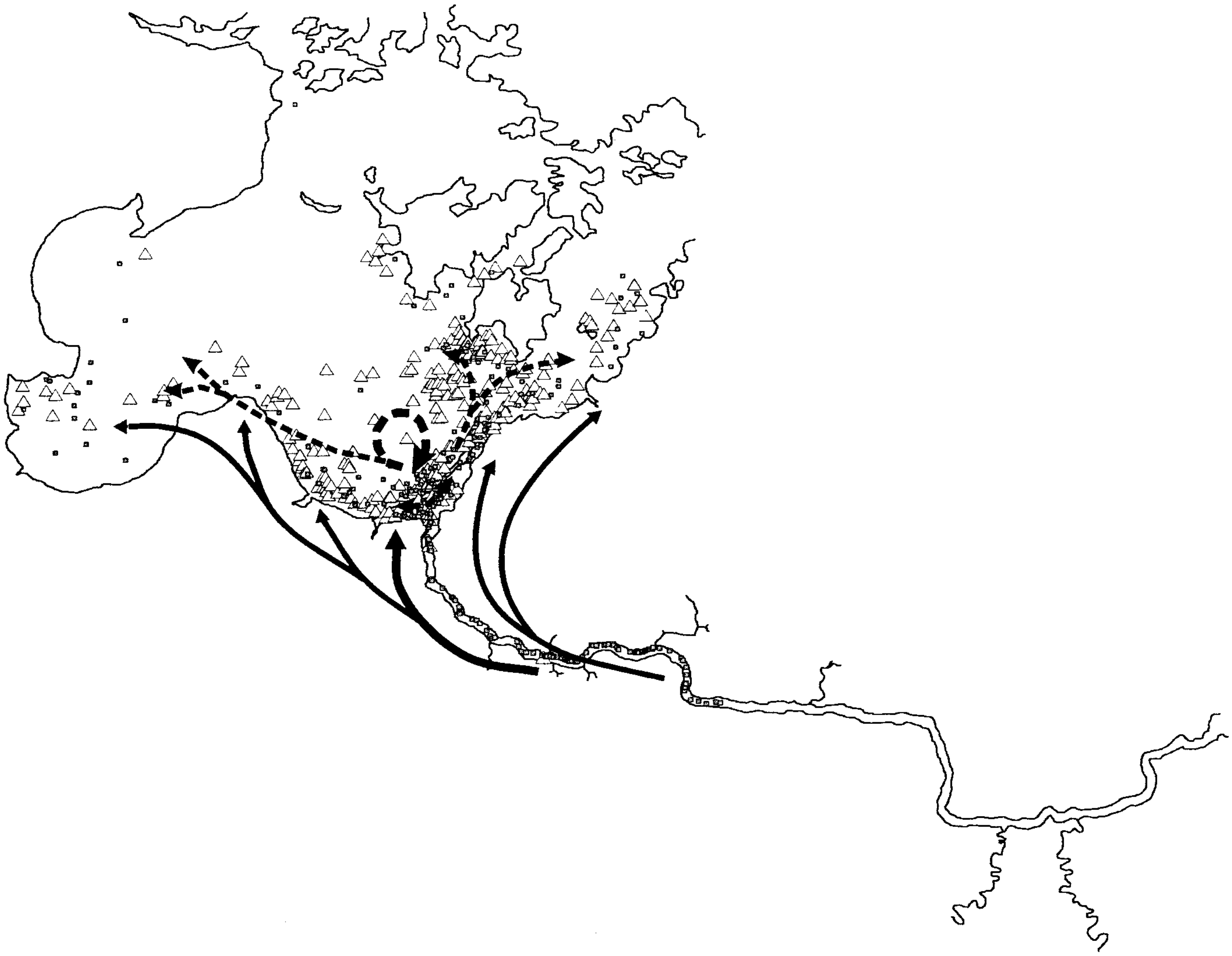


Table 3. Movement rates (km/day) and calculated significance levels for one-way ANOVAs of seasonal and combined movement rates, grouped by overwintering habitat and by sex; the last column summarizes information for all fish in a given season.

	River fish	Lake fish	*p*	Males	Females	*p*	All fish	*n*
Spring	0.955 (0.66)	0.732 (0.67)	0.007	0.776 (0.67)	0.940 (0.67)	0.056	0.840 (0.67)	517
Summer	0.739 (0.55)	0.779 (0.57)	0.638	0.786 (0.57)	0.706 (0.53)	0.366	0.758 (0.56)	340
Fall	0.520 (0.46)	0.438 (0.41)	0.171	0.460 (0.45)	0.525 (0.40)	0.262	0.492 (0.43)	352
Winter	0.080 (0.11)	0.149 (0.15)	0.000	0.121 (0.13)	0.102 (0.13)	0.254	0.114 (0.13)	308
All seasons	0.579 (0.59)	0.555 (0.55)	0.504	0.556 (0.56)	0.586 (0.58)	0.425	0.567 (0.51)	1517

Note: Values are given as the mean, with the standard deviation in parentheses.

test). Similarly, when habitat and sex were analyzed individually by season, there were no significant differences among river and lake fish during the spring and summer (Table 3). The largest between-habitat difference in movement rates occurred during winter months, when lake fish moved more quickly than river fish. The opposite relationship was observed in the spring, when river fish were more active. The highest movement rates occurred in the spring and the lowest in the winter (Table 3).

The seasonal differences in monitoring frequency (twice per week in the spring, weekly in the summer, twice per month in the fall, monthly in the winter) we employed have the potential to confound among-season comparisons of movement rates (within-season comparisons would be unaffected).

Fig. 6. Summer movement patterns of lake sturgeon during 1988–1990 in Lake of the Woods and the Rainy River. Open triangles and broken lines represent individual locations and generalized movements of lake fish. Shaded squares and solid lines indicate corresponding observations for river fish.

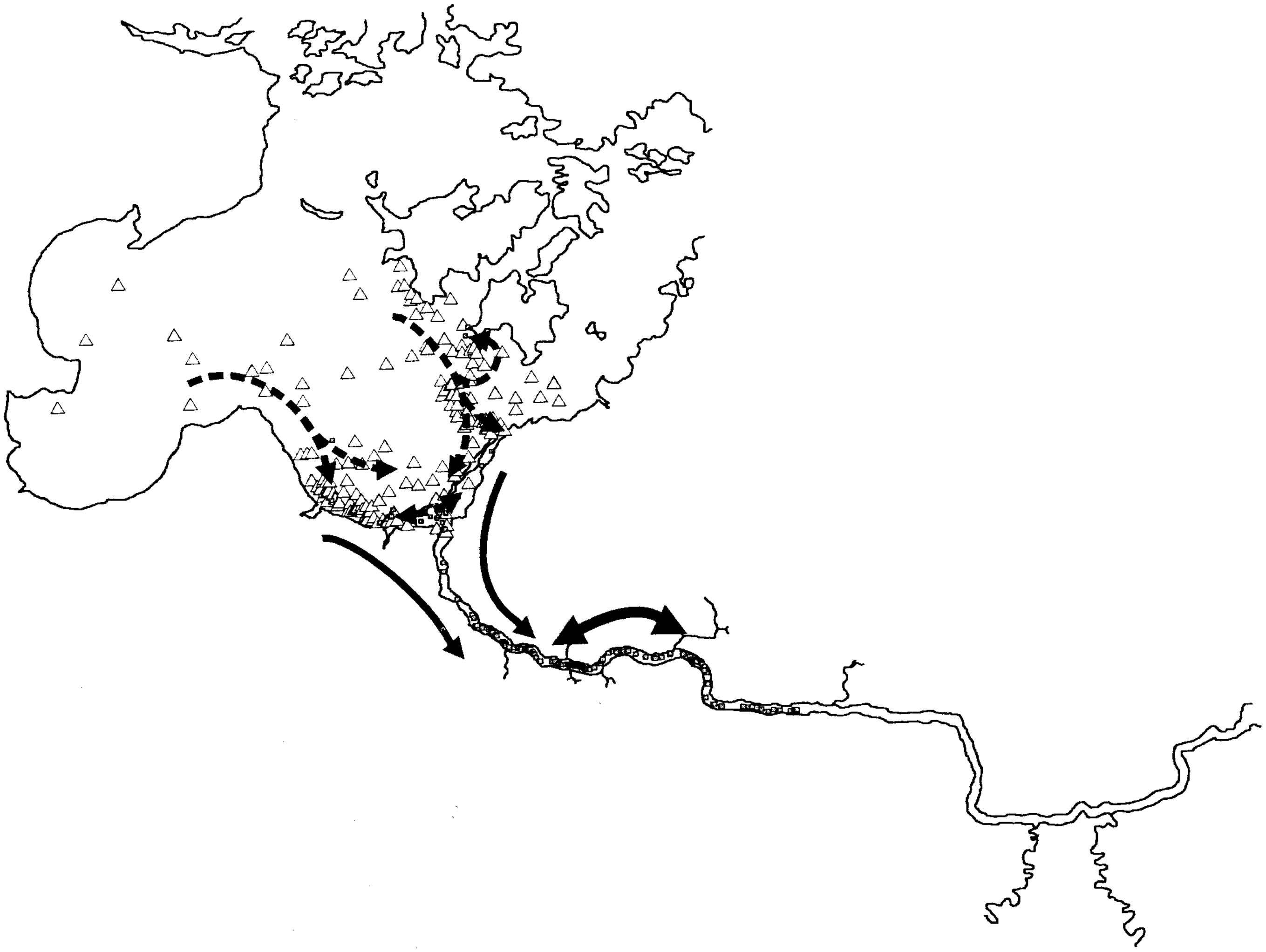
Movement rates were calculated on a per-day basis, and increasing the interval between successive monitoring events could alone decrease the calculated movement rate. However, this can only occur when movements are random; if they are directional, as we have demonstrated for all seasons with the possible exception of winter, comparisons among seasons will be valid. Furthermore, the bias introduced when movements are random is greatest when sampling varies among the first 1–5 days (i.e., the relationship between movement rate and sampling interval declines almost exponentially and soon becomes asymptotic to the *x* axis). The mean intervals between flights by season were as follows: 6.9 days (SD = 3.6 days) in the spring; 10.6 days (SD = 5.9 days) in the summer; 11.4 days (SD = 5.4 days) in the fall; 21.4 days (SD = 13.4 days) in the winter. These differences between proposed and actual monitoring frequency exist because the "seasons" we used to analyze fish movements were based strictly on individual dates determined by changes in water temperature, while the seasonal changes in monitoring frequency were more subjective, determined more by a yearly anticipation of change. Thus, many of the late "winter" fixes were actually done on a weekly basis as the weather began to warm in the spring (over half of the calculated movement rates came from monitoring intervals of 15 days or less). Similar situations arose for the other seasons. This is also evident in the near equitable distribution of the total numbers of locations used to calculate mean movement rates among seasons (Table 3). We suggest that any bias in the winter movement rates that might be related to differences in monitoring frequency is minimal.

Spawning migrations

All radio-tagged lake sturgeon moved upriver to spawning grounds only in the year in which they were ready to spawn. Resting adults that had been radio-tagged prior to the spawning season were not observed migrating upstream along with ripe adults. Of the eight females that were radio-tagged, only one was tracked upstream during the spring. This fish was also observed to have the largest eggs at the time of capture; they were of a size above the range necessary for spawning (Guénette et al. 1992).

Spawning dates varied considerably among years. Spawn-

Fig. 7. Fall movement patterns of lake sturgeon during 1988–1990 in Lake of the Woods and the Rainy River. Open triangles and broken lines represent individual locations and generalized movements of lake fish. Shaded squares and solid lines indicate corresponding observations for river fish.



ing was completed on the Little Fork River by the end of the first week in May in 1987 (Eric Anderson, Minnesota Department of Natural Resources (DNR), St. Paul, personal communication). Spawning dates for fish identified from the lake group ranged from the middle of May in 1988 to the start of June in 1990.

Spawning migration is thought to be initiated by increases in water temperature in early spring (Scott and Crossman 1973). In our study, two male river sturgeon commenced upstream movement in 1990, as soon as water temperatures began to rise above 5–6°C, and were on the spawning grounds at temperatures of 11–13°C. In the same spring, two male lake sturgeon did not start upstream migration to the same spawning grounds until river temperatures had reached 12°C. These fish arrived at the spawning grounds when temperatures were 13–14°C. No appreciable differences in migration and spawning temperatures (i.e., spawning at 13°C; migration at 12–12.5°C) were observed between the river (i.e., two males) and lake (i.e., four males) fish that were tracked upstream in 1989. However, all of these fish had undergone transmitter implantation just prior to spawning and this may have affected subsequent behaviour. The two river fish both moved downstream, initially for 8–12 days, before resuming upstream migration. Three of the four lake fish either remained in the tagging area during the same period or continued upstream. Only one radio-tagged fish from the lake population exhibited downstream movement. In 1988, six migrating sturgeon that were radio-tagged and later identified as lake fish were tracked to upstream spawning grounds. They appeared to commence migration and spawning at river water temperatures of 12.5°C (range 12–13°C) and 13.5°C (range 12–15°C).

Evidence of "homing behaviour" among lake sturgeon in this study was contradictory. Of the two male lake sturgeon followed onto upstream spawning grounds in the springs of 1988 and 1990, one fish returned to the same location in both years, while the second fish did not. Further evidence, both for and against homing behaviour, was inferred from observed movements onto the two most frequented spawning grounds: below the dam on the Rainy River at the outflow of Rainy Lake and at Flat Rock Rapids, a set of three dispersed rapids on the Little Fork River. Only one fish, a river male, was tracked to both sites in the spring of 1990. Its farthest observed upstream movement was to Flat Rock Rapids, 46 km up the Little Fork River. It then returned to the Rainy River, where it proceeded upstream to just below the Rainy River dam. These two spawning grounds are separated by a river distance of about 93 km. All other fish, tracked at least as far as the confluence of the Little Fork and Rainy rivers, appeared to limit spawning migrations to either one or the other site. However, radio-tagged fish were often located at a set of rapids (either Long Sault or Manitou) on the Rainy River en route to spawning grounds with a frequency that seemed to be much greater than that due to chance alone.

Discussion

Lake sturgeon movements in the Rainy River – Lake of the Woods system appear to be partitioned along winter habitat preferences. Fish which returned annually to overwinter in the Rainy River were distinct, in terms of spawning migrations and seasonal movement patterns and rates, from those that remained in the lake. Differences in movement might be a function of spawning periodicity and prespawning behaviour, with subsequent patterns related to a multiyear rotation between pre- and post-spawning habitats. However, the evidence suggests that observed differences in lake sturgeon movements are a result of the presence of two distinct populations in this area. While no other populations were identified during our study, their existence cannot be discounted without further investigation.

Our results are based on transmitted locations of radio-tagged sturgeon that were tracked regularly for almost 3 years. We feel that both the multiyear duration of this study and our ability to pinpoint the location of radio-tagged fish during each tracking event have provided an accurate assessment of lake sturgeon movement in this area. The coherence of movement patterns, of both groups and individuals, among consecutive years of monitoring lends further credibility to our observations.

Seasonal movements

Lake sturgeon moved least in the winter, remaining aggregated in relatively distinct areas of the lake and river. Hay-Chmielewski (1987) reported a similar behaviour pattern in Black Lake, Michigan, and hypothesized that restricted movement during the winter months may be a foraging response to food concentration. Overwintering areas on the Rainy River were located along the lower stretches of the river, from Pinewood to the river mouth (Fig. 1), where benthic communities have shown the greatest recovery from past pollution effects associated with upstream pulp and paper mills (Beak Consultants Limited 1990). Further evidence of a year-round link between seasonal movements and foraging behaviour is provided by the fact that fish were never located above Long Sault Rapids, except for spawning.

Our data suggest that sturgeon, including lake fish, preferred areas that offered increased water movement, whether winter or summer patterns are examined. Sturgeon were most often found near peninsulas and in channels (Figs. 5–7) or at the Rainy River mouth. Extensive lake movements during late spring and early summer were also oriented along mainland and island shorelines. Few fish were ever located out in the central areas of the Big Traverse basin and other large bays. Bassett (1982) and Hay-Chmielewski (1987) found lake sturgeon mostly along sloping areas of lake bottom during both winter and summer. This habitat preference could account for the observed distribution of fish along shoreline areas at the south end of Lake of the Woods, since most of the Big Traverse basin has a fairly uniform bottom at depths of 8 – 10.5 m. We did not determine whether these areas held prey concentrations.

We found lake sturgeon most frequently at water depths of 6 m or greater in both river and lake locations throughout our study. Considerable variation in preferred depth is reported. Both Hay-Chmielewski (1987) and Williams (1951) found sturgeon in deeper waters (e.g., 6 – 13 m) during summer and winter. However, Harkness and Dymond (1961) observed lake sturgeon in shallower water in Lake Nipigon during the open-water season. Reported differences in preferred depth can likely be attributed to the importance of food in habitat selection and the variation in depth at which these foods can occur in different lakes.

The substantial between-year variation in mean temperatures at which fish entered the lake (Table 2 and Fig. 3) suggests that an increasing trend rather than any absolute temperature value is the determining factor. River flows provided a similar cue. The spring increase in flow, due to snowmelt and spring rainfall, consistently preceded the movement of river fish into the lake (Fig. 4). The later start to long-range movements by lake fish in the spring appeared to coincide with the delayed increase in lake temperature. When river fish returned in early August, the absolute temperature and flow values seemed to have little effect on triggering upstream movement, but their pattern, especially the consistent association of a summer maximum temperature with a return to the river, appeared to be the most reliable cue.

Evidence from tagging studies has supported the existence of both wide-ranging (Larson 1988; Auer 1993) and relatively restricted (Priegel and Wirth 1971; Dumont et al. 1987) seasonal movements of lake sturgeon. We suggest, based on our long-term telemetry data, that basinwide movement patterns in contiguous lake–river systems may be the most prevalent behaviour during the ice-free season, while fairly limited movements are the norm during the winter months. The coherence of observed patterns among years, and the fidelity of groups and often individuals to them, provide ample support for the existence of definite seasonal movements, as well as for distinct populations in this system.

Movement rates

Although Hay-Chmielewski (1987) found a strong positive relationship between increasing water temperature and linear movement, this was not evident in our study. The initiation of long-distance movement in the spring appeared to be related to increasing water temperature, and the highest movement rates were also observed during this season (Table 2). However, at this time the water was still considerably cooler than during late summer, when movement was slower. We did observe a decline in movement rates with decreasing water temperature.

We found no significant differences in overall movement rates among lake and river fish, but differences in seasonal movement rates, related to winter habitat preference, were evident (Table 3). Lake fish appeared to move more frequently than river fish during the winter, although they appeared to occupy similar-sized "territories" during this season. However, this may only be a relative difference, since river fish could expend the same amount of energy as lake fish simply to remain in one place in the river flow. Similarly, the earlier spring start to long-range movements of river fish could contribute to their significantly higher movement rates during the spring. However, given the large number of fixes during this period, this early start is unlikely to be the only reason for the observed differences between lake and river fish. Movement-rate differences offer further support for population differentiation.

Spawning migrations

Sturgeon movement upstream to spawning grounds on the Rainy River appeared to be initiated by increasing water temperature, since actual spawning dates and the timing of peak river flows varied during 1987–1990. The commencement of spawning migrations also varied between the two populations. Fish from the two groups likely responded to the same temperature cues for spawning, but fish that overwintered in the river would experience an earlier rise in ambient water temperature in the spring than fish in the lake. This difference could account for the observed earlier migration and spawning of river fish. Although initially it seemed unlikely that these groups could be genetically isolated, since spawning seasons overlap and the same spawning locations are used, this differential spring warming cue, over evolutionary time, could allow population segregation. Our telemetry data are supported by the observations of local residents of Little Fork, Minnesota, who annually mark the passage of two separate runs of sturgeon on the nearby Little Fork River during the spring: an earlier, smaller (river) run followed by a larger (lake) run (Mike Larson, Minnesota DNR, Baudette, personal communication). Extensive tagging studies (Priegel and Wirth 1978; Lyons and Kempinger 1992; Fortin et al. 1993) have demonstrated that segregation of spawning fish from different lakes can occur on the same spawning grounds. However, the river–lake differentiation amongst spawners that we observed has not, to our knowledge, been previously documented and may, in fact, be a prevalent phenomenon in larger systems.

Lyons and Kempinger (1992) postulated that a substantial portion of lake sturgeon spawning migration may occur during the previous fall, with fish then overwintering in the river. We did not observe this behaviour in any spawning fish from either the lake or river population. The two fish that made repeat migrations onto upstream spawning grounds in 1988 and again in 1990 both returned to the habitats they had occupied prior to spawning. Spawning fish that used either the river or the lake for overwintering were followed back to these same habitats in successive years without exception. Previous observations of fall migration into rivers may instead offer additional support for a more widespread occurrence of separate riverine stocks.

In summary, lake sturgeon in Lake of the Woods and the Rainy River displayed two distinct patterns of seasonal movements. Both patterns were consistent among years and were wide-ranging, with distinct differences in movement rates. Seasonal variation appears to be a strong structuring component of these patterns and rates. The modification of seasonal cues by differences in large-scale habitat seems to have allowed the differentiation of two populations in this system. These findings should sound a cautionary note to those who manage lake sturgeon on similar lake–river systems. Given even slight diversity of habitat structure and temporal cues, what appears to be a single population may not always behave as such. Attempts to regulate the harvest of such populations should be based on a recognition of these differences. Because lake sturgeon are capable of making extensive movements, it also becomes essential to protect and manage the full range of temporal and spatial habitat types required.

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