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[Article]

Movements of Lake Trout in U.S. Waters of Lake Superior, 1973–2001

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Abstract.—We analyzed tag–recapture data for lake trout *Salvelinus namaycush* from the U.S. waters of Lake Superior to determine whether (1) mean movement distance varied among management units, (2) mean movement distance and recapture percentage differed between spawning and nonspawning recapture seasons, (3) percentages of movements to the east and west were similar, and (4) movement distance varied with body length, sex, origin, age, or time at liberty. Mean distance moved by lake trout varied among management units. Mean movement distance was lower for fish recaptured during the spawning season than for fish recaptured during the nonspawning season for three of four tagged populations, and the spatial distribution of recapture percentages differed between recapture seasons. On average, lake trout recaptured during the nonspawning season traveled 42 km while at liberty. Lake trout tagged in two of six management units emigrated to the east and west in equal percentages, but lake trout did not emigrate from the tagging unit to other management units at equal percentages. Movement distance varied significantly with time at liberty for lake trout tagged in one management unit, but did not vary significantly with length, age, time at liberty, sex, or origin for those tagged in other management units. Lake Superior fishery managers can use our results to account for lake trout movements between management units when calculating sustainable harvest levels with catch-at-age modeling.

Managers of animal populations have increasingly recognized movements as important to the life history, evolution, and population dynamics of most animal species (Lidicker and Caldwell 1982). Movements are often associated with attaining the maximum amount of food or habitat while avoiding predation and other sources of mortality (McCormick et al. 1998). Movement can affect population dynamics by adding to or subtracting from a population, thereby altering species abundance, interactions, and genetic variability (Primack 1998; Turchin 1998). Movement is especially important to consider in the management of inland fisheries because fish movements can affect all three areas of the current fisheries management paradigm: organisms, habitats, and people (Kohler and Hubert 1993).

Movement of lake trout *Salvelinus namaycush* in Lake Superior has been studied since the 1950s (Eschmeyer et al. 1953; Loftus 1958; Pycha et al. 1965) to better understand and manage this ecologically and economically valuable species (Eschmeyer 1964; Smith 1972; Hansen et al. 1995; Schram and Fabrizio 1998). Lake trout are long-lived (Schram and Fabrizio 1998) and act as apex predators of the coldwater fish community in Lake Superior (Smith 1972). Lake trout in Lake Superior are highly mobile (Eschmeyer et al. 1953; Rahrer 1968) but have a strong homing behavior during the spawning period (Eschmeyer 1964; Swanson 1973; Krueger et al. 1986). Mean distance traveled by hatchery-reared and wild-born lake trout in Lake Superior has been reported to vary from 14 km (Buettner 1961) to 108 km (Eschmeyer 1955). Lake trout movement may vary with fish length (Eschmeyer et al. 1953; Peck 1981), age (Pycha et al. 1965), sex (Eschmeyer 1955), origin (hatchery-reared versus wild-born; Swanson 1973; Krueger et al. 1986), and time at liberty (Eschmeyer et al. 1953; Buettner 1961). Hatchery-reared lake trout returned to spawning reefs in smaller proportions than did wild-born lake trout (Swanson 1973; Krueger et al. 1986), and wan-

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dering of hatchery-reared lake trout may reduce their spawning potential (Swanson 1973).

Fishery managers use catch-at-age models to estimate safe harvest levels of lake trout in specific management units of Lake Superior, but these models assume that movement of lake trout between management units is approximately equal and that movement does not vary with length, age, time at liberty, sex, and origin. However, lake trout that move across jurisdictional boundaries are subjected to different levels of fishing pressure and exploitation because fishery regulations vary among jurisdictions (Rahrer 1968; Hansen et al. 1995). If, for example, hatchery-reared lake trout move greater distances than wild-born lake trout, they would be more likely to travel across jurisdictional boundaries and thus would be subjected to different regulations and levels of exploitation. Harvest levels may be set too high and overfishing may occur if movement of lake trout between management units subjects them to excessive fishery exploitation.

Our objectives were to determine whether (1) mean distance moved by lake trout varied among management units, (2) mean movement distance and recaptures per unit of recapture effort differed between spawning and nonspawning recapture seasons, (3) lake trout recaptured during the nonspawning season emigrated to the east and west at equal rates, and (4) movement distance varied with body length, sex, origin, age, or time at liberty (months). For our first objective, we expected that mean distance moved by lake trout would vary among management units due to behavioral differences among fish tagged in different areas of the lake. For our second objective, we expected to find that lake trout would be recaptured at higher rates near the spawning reefs where they were originally tagged, thereby yielding smaller mean distances moved and higher recapture rates near spawning areas during the spawning recapture season than during the nonspawning recapture season. For our third objective, we expected that lake trout would emigrate to the east and west in equal percentages, that most lake trout would be recaptured in the management unit where they were originally tagged, and that recapture rates from other management units would decrease with increasing distance from the tagging unit. For our fourth objective, we expected to find greater movement distances by large lake trout than small lake trout (Eschmeyer et al. 1953), shorter movement distances by males than females (Eschmeyer 1955; MacLean et al. 1981), greater movement distances

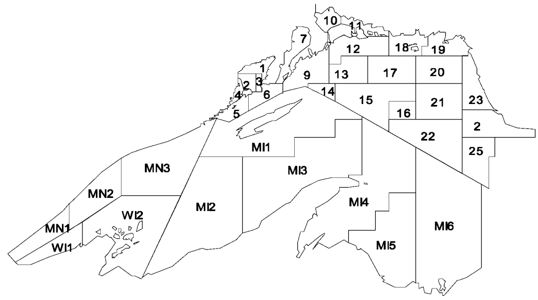

FIGURE 1.—Lake Superior lake trout management units. U.S. management units are denoted by state: MI = Michigan; MN = Minnesota; WI = Wisconsin. Units marked by numbers only are in Canadian waters.

by hatchery-reared than wild-born lake trout (Swanson 1973; MacLean et al. 1981; Krueger et al. 1986), greater movement distances by old lake trout than young lake trout (Pycha et al. 1965), and a positive relation between movement distance and time at liberty (Eschmeyer et al. 1953; Buettner 1961).

Methods

Tagging and recapture.—Data were obtained from lake trout tagged and released in Wisconsin management units WI-1–2 and Michigan management units MI-2–5 (Figure 1). Data from lake trout tagged in Minnesota and Canada were not included because too few recaptures were reported. Lake trout in Lake Superior were captured for tagging with trap nets and monofilament or nylon gill nets of various stretch measures; six different management agencies conducted the tagging (Table 1; Kapuscinski 2002). Nets were fished during spring, summer, and fall in 1973, 1976, and 1980–2000. Date, location, tag number, and biological information (total length, sex, and fin clip indicating hatchery origin) were recorded for each tagged lake trout. The sex of live lake trout was determined by visual examination during the spawning season, and the sex of dead lake trout was determined by dissection. Lake trout were tagged with individually numbered Floy anchor tags that provided contact information for the tagging agency. Floy tags were secured near the middle and base of the dorsal fin, and all tagged fish were promptly released near their capture locations.

Lake trout were recaptured in angling and gillnet fisheries (commercial fisheries and spring, summer, and fall assessment surveys) during 1973 and 1984–2001. Survey fisheries were operated by seven agencies at numerous sites across the U.S.

TABLE 1.—Gears used by the Great Lakes Indian Fish and Wildlife Commission (GLIFWC), Keweenaw Bay Indian Community (KBIC), Red Cliff Fisheries Department (RCFD), Michigan Department of Natural Resources (MDNR), Wisconsin Department of Natural Resources (WDNR), and U.S. Geological Survey (USGS) to capture lake trout in Lake Superior during 1973–2000 for tagging and release. All lake trout were tagged with Floy tags near the base of the dorsal fin.

Agency	Tagging year(s)	Survey gear type	Gill-net stretch measure (cm)
GLIFWC	1988–1998	Multifilament gill net	11.43, 12.7, 13.97
KBIC	1993–1998, 2000	Multifilament gill net	11.43, 12.7, 13.97
MDNR	1973	Trap net	
MDNR	1976, 1983–1987	Gill net	3.81–6.4, 11.40–15.19
RCFD	1984–1999	Gill net	5.08–15.24
WDNR	1980–2000	Multifilament or monofilament gill net	3.81–17.78
USGS	1985–1998	Gill net	

waters of Lake Superior. Otoliths were extracted from dead, survey-recaptured lake trout to estimate ages of recaptured fish. Information and tags from lake trout recaptured in angling and gill-net fisheries in Lake Superior were returned voluntarily, usually via telephone, mail, or in person. The Great Lakes Indian Fish and Wildlife Commission offered a US$5.00 reward for the return of their tags and the accompanying information.

Data analysis.—We analyzed data from lake trout tagged during the fall spawning season (October or November) at or near spawning reefs, and we considered lake trout tagged in the same management unit to be part of the same tagged population. Recaptures from spawning and nonspawning (December–September) seasons were kept separate during analysis because lake trout have strong homing instincts, and movement of lake trout recaptured in spawning areas during the spawning season would differ from movement of lake trout recaptured during the nonspawning season. Records of recaptured, tagged lake trout included (1) matching tag numbers at time of tagging and recapture, (2) tagging and recapture dates, and (3) tagging and recapture locations. Recapture locations were reported with varying levels of precision, so we used only recaptures reported at least to the nearest statistical grid, generally a 10- × 10-min latitude-by-longitude grid used by fishery agencies in the Great Lakes to record location. Lake trout were assigned to a recapture management unit for analysis based on their reported recapture location (multiple statistical grids occur in any one management unit).

Mean distance moved.—We combined recaptures from agency gill-net surveys and commercial gill-net fisheries because capture gears were nearly identical. We assumed that reporting rates differed among recapture fisheries but were consistent among management units within each fishery. Variation in reporting rates could only bias movement estimates if reporting rates varied among locations for any recapture fishery. We also assumed that catchability did not vary among management units for either commercial or angling fisheries. We assumed that commercial fisheries primarily targeted lake whitefish *Coregonus clupeaformis* and secondarily targeted lake trout in all management units, but that this pattern was consistent among management units.

A vector-based geographic information system was used to calculate the distance and direction moved by each lake trout. The x- and y-coordinates for the center of each statistical grid were used to calculate the Euclidian distance traveled (D) by each lake trout from the grid of tagging to the grid of recapture, that is

$$D = \sqrt{(x_1 - x_2)^2 + (y_1 - y_2)^2}$$

Migration routes are rarely straight-line movements between tagging and recapture areas (Schwarz and Arnason 1990; Turchin 1998), so the use of Euclidian distance provided a minimum estimate of distance moved by each lake trout. The minimum distance between two adjacent grids was 9.42 km.

When the number of reported recaptures from a tagged population was large enough ($N \geq 30$), mean distance moved (km) was estimated and the 95% confidence interval about the mean was calculated (Milton and Arnold 1995). Lake trout recaptures were separated by spawning and nonspawning recapture seasons, and the mean distance moved was compared among tagged populations by use of a single-factor analysis of variance (ANOVA). A single-factor ANOVA was also used to compare mean distance moved between spawning and nonspawning recapture seasons for lake trout from each tagged population. Tukey's pairwise comparison test was used to determine which means were significantly different from one another ($P \leq 0.05$).

Movements between management units.—Recapture distributions can be biased by spatial and temporal variation in recapture effort (Schwarz and Arnason 1990), so we sought to reduce these biases by standardizing recaptures to the amount of annual recapture effort within each management unit. Total annual recapture effort for angling (angler-hours) and gill-net (ft of net) fisheries was estimated for each management unit by each fishery agency (Tables 2, 3). Recaptures were separated by recapture fishery (angling or gill-net fishery), recapture season (spawning or nonspawning), and the management unit in which the lake trout were originally tagged (tagged population). Percent movement was quantified for each tagged population (e.g., percent movement of lake trout tagged in WI-1 was quantified separately for angling recaptures and gill-net recaptures). Recaptures per unit effort (RPE) from both angling and gill-net recapture fisheries were estimated for each tagged population as follows:

$$\sum \text{RPE}_{\text{tp}} = \frac{R_{\text{mu}-x}}{E_{\text{mu}-x}} + \frac{R_{\text{mu}-y}}{E_{\text{mu}-y}} + \cdots + \frac{R_{\text{mu}-z}}{E_{\text{mu}-z}};$$

where $\Sigma\text{RPE}_{\text{tp}}$ is the number of RPE for tagged population TP, $R_{\text{mu}-x}$ is the number of reported recaptures in management unit x in a given year, and $E_{\text{mu}-x}$ is the amount of recapture effort in management unit x in that year. Percent movement from the management unit where population TP was tagged to management unit x was estimated as

$$\text{MU}_{\text{tp}} \rightarrow \text{MU}_x = \frac{(R_{\text{mu}-x}/E_{\text{mu}-x})}{\sum \text{RPE}_{\text{tp}}};$$

where MU_{tp} is the management unit where the population was tagged and MU_x is the management unit to which lake trout emigrated.

Recapture rates (RPE) for lake trout tagged in WI-2 and MI-3–4 and recaptured in gill-net fisheries were compared between spawning and nonspawning seasons by use of a chi-square test ($P \leq 0.05$). Seasonal comparisons of recapture rates for the angling fishery were not possible because too few lake trout were recaptured during the spawning season (angling fisheries are generally closed during months when lake trout spawn).

Movement percentages, estimated separately for angling and gill-net fisheries from nonspawning season recaptures, were averaged to obtain mean percent movement for each tagged population except for lake trout tagged in MI-3. Movement percentages for lake trout tagged in MI-3 were calculated only from recaptures in the gill-net fishery because too few tagged lake trout were recaptured in the angling fishery there. The confidence interval (95%) for mean percent movement was estimated for each tagged population (Milton and Arnold 1995).

To test whether lake trout emigrated to the east and west at similar rates, the proportion of RPE obtained in management units to the east of the tagging management unit were compared to an expected proportion of 0.50 (Milton and Arnold 1995), as follows:

$$Z = \frac{P_E - 0.50}{\sqrt{\dfrac{P_E(1 - P_E)}{N}}},$$

where Z is the test statistic, P_E is the proportion of RPE in management units to the east of the tagging management unit, and N is the number of lake trout that emigrated east or west. If Z was less than -1.96, we inferred that lake trout emigrated at a greater percentage to the west than to the east. Conversely, if Z was greater than 1.96, we inferred that lake trout emigrated at a greater percentage to the east than to the west. We did not test for emigration to the north or south because we assumed lake trout inhabited depths less than 92 m (Eschmeyer 1964; Pycha et al. 1965) and followed bottom contours while emigrating, thereby restricting their movement to the east or west along shorelines (Pycha et al. 1965). Lake trout tagged in WI-1 and recaptured in Minnesota waters (MN-1–3) or in MI-1 were assumed to have emigrated along the shoreline, and we considered this movement to be westward to simplify the reporting of our findings. Furthermore, emigration to the south was possible in few locations (Figure 1).

Factors associated with movement distance.—We expected distance moved to be a multiplicative function of body length, age, time between tagging and recovery, origin, and sex, so we modeled total distance moved (D_i) for lake trout of each tagged population as a nonlinear function of total length (L, mm), age (A, years), time at liberty (T, months), origin (O, wild-born or hatchery-reared), and sex (S, male or female), where adequate numbers of recaptures were obtained ($N \geq 30$ for each variable), as follows:

TABLE 2.—Total annual lake trout angling effort (angler-hours) in U.S. waters of Lake Superior by management unit and year, as estimated by fishery agencies during 1982–2000.

Year	Management unit					
	MN-1	MN-2	MN-3	WI-1	WI-2	MI-1
1982				46,013	141,630	
1983				41,654	105,450	
1984				32,024	143,811	
1985				31,161	130,450	
1986				29,823	90,944	
1987				97,091	116,283	
1988	252,219	34,334	46,273	80,225	148,229	
1989	207,138	49,828	23,111	71,474	157,226	
1990	205,316	44,072	27,141	63,071	123,621	496
1991	182,665	40,252	16,729	62,346	128,164	5,102
1992	170,000	35,000	28,000	61,430	92,672	5,710
1993	130,000	28,000	27,000	74,984	83,370	4,857
1994	102,220	19,858	25,765	49,774	127,177	5,479
1995	108,572	17,846	31,111	58,956	101,055	3,731
1996	127,298	10,201	23,668	49,693	97,400	5,139
1997	107,057	4,266	27,199	33,394	214,525	3,671
1998	114,021	5,667	22,908	39,174	108,575	3,427
1999	116,571	10,035	22,110	43,171	172,592	4,179
2000	135,996	17,842	18,821	29,307	132,775	4,179

$$D_i = \beta_0 X_i^{\beta_x} e^{\varepsilon},$$

where β_0 is the mean distance moved, X_i are variables for length, age, time at liberty, origin, and sex (L, A, T, O, or S), β_X are coefficients that describe how mean movement distance varied with length, age, or time at liberty, or differed between origins or sexes, and ε is unexplained variation. The model was $\log_e$ transformed to normalize the residuals, and a value of 1 was added to each observation of D_i to account for observed values equal to 0 (lake trout recaptured in the same grid in which they were tagged), namely,

$$\log_e(D_i + 1) = \log_e(\beta_0) + \beta_x \cdot \log_e(X_i) + \varepsilon_i.$$

All variables X_i were tested for significance by use of a general linear model. If more than one variable was significantly related to D_i ($P \leq 0.05$), then interactions between significant variables were tested for significance ($P \leq 0.05$).

Results

Of the 44,640 lake trout tagged in management units WI-1–2 and MI-2–5, 1,758 were recaptured in angling and gill-net fisheries. Recaptured lake trout averaged 610 mm in length (range = 340–874 mm) at the time of tagging and 11 years of age (range = 4–25 years) at the time of recapture. Lake trout were recaptured from January to December in 1973 and 1984–2001, and recaptures were made in all U.S. management units except MI-8.

Lake trout recaptured during the nonspawning season in gill-net and angling fisheries moved an average of 42 km (SD = 48.76 km; range = 0–297 km; $N = 890$; Table 4). Mean distance moved by lake trout recaptured during the nonspawning season varied among tagged populations ($F = 13.21$; df = 5, 884; $P < 0.001$; Table 4). Mean distance moved by fish recaptured during the nonspawning season was significantly lower for lake trout tagged in MI-4 than for those tagged in WI-1–2 and MI-2–3 (Tukey's test, $P < 0.0052$), but the values for MI-4 and MI-5 did not differ (Tukey's test, $P = 0.1623$).

Lake trout recaptured during the spawning season in gill-net and angling fisheries moved an average of 17 km (SD = 37.82 km; range = 0–254 km; $N = 543$; Table 5). Mean distance moved by lake trout recaptured during the spawning season varied among tagged populations ($F = 44.82$; df = 3, 539; $P < 0.001$) and was significantly lower in WI-2 than in MI-3 (Tukey's test, $P < 0.0008$) or MI-5 (Tukey's test, $P < 0.0001$). Mean distance moved during the spawning season was also significantly lower in MI-3 and MI-4 than in MI-5 (Tukey's tests, $P < 0.0001$).

Mean distance moved by lake trout recaptured in gill-net and angling fisheries differed between spawning and nonspawning seasons for lake trout tagged in WI-2 ($F = 94.77$; df = 1, 598; $P < 0.001$), MI-3 ($F = 30.10$; df = 1, 156; $P < 0.001$), MI-4 ($F = 19.18$; df = 1, 478; $P < 0.001$), and MI-5 ($F = 9.44$; df = 1, 89; $P < 0.003$) (Table

TABLE 2.—Extended.

Year	MI-2	MI-3	MI-4	MI-5	MI-6	MI-7	MI-8
	Management unit						
1982							
1983							
1984						19,990	
1985						25,529	
1986						35,163	
1987	52,800		12,800	82,900	19,400	25,288	
1988	51,600		13,900	66,900	32,100	16,136	
1989	47,000		30,000	70,000	38,000		
1990	9,251	242	3,116	7,597	1,370	16,132	
1991	56,042	4	48,314	97,649	73,857	23,501	
1992	59,277	348	64,175	96,212	92,598	23,943	
1993	61,096	466	98,188	83,637	79,288	19,859	
1994	28,729	708	127,436	66,149	72,691	14,733	
1995	52,087	583	69,186	54,850	46,557	13,545	
1996	52,732	502	90,981	61,344	55,970	15,034	
1997	36,591		48,266	74,746	59,293	17,917	
1998	31,734	200	41,326	59,644	50,457	13,364	321
1999	32,000		35,000	68,330	35,000	13,281	
2000	30,000		20,000	68,330	30,000	12,255	

6). In WI-2, MI-3, and MI-4, the mean distance moved by lake trout was greater for nonspawning season recaptures than for spawning season recaptures, whereas in MI-5 the mean distance moved was greater for spawning season recaptures than for nonspawning season recaptures (Table 6). Recapture rates (RPE) in the gill-net fishery differed between spawning and nonspawning seasons for lake trout tagged in WI-2 ($P < 0.0001$), MI-3 ($P < 0.0151$), and MI-4 ($P < 0.0001$).

Most lake trout tagged in WI-1 and MI-2–5 and recaptured in angling and gill-net fisheries during the nonspawning season remained in the management unit in which they were tagged, and emigration to other management units generally decreased with distance from the tagging management unit (Table 7). Most lake trout tagged in WI-2 were recaptured in WI-1. Lake trout tagged in WI-2 ($Z = -5.28$; $N = 317$; $P < 0.0002$) and MI-5 ($Z = -14.13$; $N = 59$; $P < 0.0002$) moved in greater percentages to the west than to the east, lake trout tagged in WI-1 ($Z = 2.27$; $N = 37$; $P = 0.0058$) and MI-4 ($Z = 2.37$; $N = 337$; $P = 0.0045$) moved in greater percentages to the east than to the west, and lake trout tagged in MI-2 ($Z = 0.89$; $N = 67$; $P = 0.0934$) and MI-3 ($Z = 1.92$; $N = 66$; $P = 0.0137$) moved to the east and west in equal percentages (Table 7).

Distance moved was positively related to time at liberty for lake trout tagged in MI-4 but was not significantly related to length, age, time at liberty, origin, or sex for other tagged populations (Table 8; Figure 2). Relations between length and distance moved in MI-2, MI-3, and MI-5; age and distance moved in MI-2–5; origin and distance moved in MI-2, MI-3, and MI-5; and sex and distance moved in MI-2–5 could not be tested because too few recapture records were available for analysis.

Discussion

Mean Distance Moved

We found that the mean distance moved by lake trout tagged during the spawning season and recaptured during the nonspawning season (42 km) was generally similar to the results of other studies of movement by hatchery-reared lake trout in Lake Ontario (≤62 km, Elrod 1987), Lake Superior (40.23 km for most fish at liberty 3 months or less, 64.36 km for fish at liberty 2 years or more, Buettner 1961; <8 km, Pycha et al. 1965), and Lake Michigan (90% of recaptures within 68.4 km, Schmalz et al. 2002), and wild-born lake trout in Lake Superior (90% of recaptures within 80.45 km, Eschmeyer et al. 1953; <48.27 km, Loftus 1958; <53.1 km, Rahrer 1968). Eschmeyer et al. (1953) and Buettner (1961) concluded that most lake trout tended to remain near release locations regardless of how long they were at liberty. Movements of lake trout may be limited by the species' strong homing instinct (Eschmeyer 1955, 1964; Swanson 1973). Most lake trout in our study, as well as those tagged during studies by Loftus

TABLE 3.—Total annual gill-net effort (feet of net; 1 ft = 30.5 cm) in U.S. waters of Lake Superior by lake trout management unit and year, as estimated by fishery agencies during 1980–2001. No data were available for MI-1.

	Management unit					
Year	MN-1	MN-2	MN-3	WI-1	WI-2	MI-2
1980		94,250	179,090	131,600	3,664,700	
1981		125,750	180,640	772,900	3,320,600	
1982	8,509	81,750	164,000	252,000	3,345,000	
1983	8,750	113,700	239,490	372,800	2,757,200	
1984	9,250	118,000	233,425	295,400	5,190,900	
1985	13,500	99,195	120,000	381,200	7,125,900	42,200
1986	11,000	87,800	124,854	82,700	5,538,800	121,600
1987	401,515	632,757	570,979	640,800	7,377,800	618,500
1988	323,800	629,325	704,830	489,000	8,088,200	131,200
1989	187,605	559,375	847,905	541,900	10,225,800	202,750
1990	283,280	402,975	938,645	423,800	12,040,600	164,400
1991	242,880	400,620	886,599	270,900	6,049,800	154,800
1992	325,980	401,485	980,475	311,950	4,452,975	407,500
1993	210,210	374,040	678,580	406,325	4,093,175	431,800
1994	146,220	308,800	688,560	188,800	4,492,126	177,400
1995	199,190	304,380	880,310	332,315	3,790,715	205,200
1996	128,880	318,300	713,850	175,890	3,166,760	111,200
1997	212,820	386,880	773,840	209,000	3,579,315	189,300
1998	125,140	380,875	717,180	142,700	2,977,200	93,800
1999	130,915	430,350	1,017,980	144,300	3,077,327	190,500
2000	142,380	415,315	1,005,950	127,100	2,659,500	402,800
2001	130,125	413,735	833,875			8,000

(1958), Rahrer (1968), and Schmalz et al. (2002), were tagged on or near spawning grounds. Given the strong spawning site fidelity of lake trout (Eschmeyer 1955; Swanson 1973; Ebener 1990; Mattes, in press), those that emigrate must still spend much of their time moving away from and returning to spawning grounds (Eschmeyer 1955; Rahrer 1968), which increases time spent near the tagging area and would perhaps explain why most tagged lake trout in the Great Lakes were recaptured within 81 km of their initial tagging sites.

We found that mean distance moved varied among tagged populations for fish recaptured during both spawning and nonspawning seasons, which is consistent with previous studies that have documented the presence of discrete lake trout spawning stocks in different areas of Lake Superior (Loftus 1958; Goodier 1981; Ebener 1990; Mattes, in press). Our results are also consistent with the finding that lake trout may exhibit different movement patterns based on the area of the lake where they were tagged (Pycha et al. 1965). We found that of the lake trout recaptured during the nonspawning season, those tagged in MI-4 moved a shorter mean distance than those tagged in WI-1, WI-2, and MI-3 but not MI-5. However, of the lake trout recaptured during the spawning season, those tagged in WI-2, MI-3, and MI-4 moved a shorter mean distance than those tagged in MI-5. Our findings generally agree with those of Pycha et al. (1965), who reported that hatchery-reared lake trout released in MI-4 tended strongly to remain in the area, and about 95% of the recaptures were made at or near the release area. The mean distance moved by hatchery-reared lake trout was apparently lower for fish released in M-4 than for those released in WI-2 or MI-5, where 69% and 18.5% of the recaptures were made at or near the release area (Pycha et al. 1965).

Seasonal Differences

We found that the mean distance moved by lake trout was generally greater for nonspawning season recaptures than for spawning season recaptures, which is consistent with other studies in Lake Superior that showed movement of lake trout away from spawning reefs after November (Rahrer 1968) but strong spawning site fidelity in subsequent years (Swanson 1973; Ebener 1990; Mattes, in press). We also found that RPE distributions differed by recapture season for lake trout tagged in WI-2, MI-3, and MI-4. Lake trout in our study were tagged during the spawning season, presumably at or near spawning reefs, so nonspawning season recaptures were more likely to occur away from spawning reefs than recaptures made during the spawning season. This would explain the between-season differences in mean distance moved and RPE distribution for lake trout tagged in WI-2, MI-3, and MI-4. We cannot explain, how-

TABLE 3.—Extended.

Year	Management unit MI-3	MI-4	MI-5	MI-6	MI-7	MI-8
1980						
1981			19,800	1,511,800	347,200	5,620,600
1982			11,000	2,498,500	352,000	3,805,300
1983			225,300	4,166,800	1,247,400	4,720,300
1984			366,600	3,223,400	837,000	6,553,600
1985	2,475,200	1,128,575	14,700	2,751,100	4,136,400	4,091,400
1986	3,097,200	5,068,600	208,000	2,458,000	4,192,000	6,212,900
1987	2,536,600	5,105,090	509,000	2,132,800	3,617,100	7,865,400
1988	2,603,700	6,081,580	578,900	2,360,800	3,975,300	9,112,800
1989	1,678,400	7,052,780	239,900	2,422,400	4,476,900	13,190,100
1990	2,145,900	9,085,501	726,400	2,323,400	5,478,600	15,678,900
1991	1,470,400	6,865,700	391,900	2,154,400	4,338,100	11,646,700
1992	1,795,600	6,367,275	533,400	1,582,400	2,584,100	10,554,520
1993	2,195,100	4,838,209	434,900	670,400	2,789,000	7,585,300
1994	1,764,200	3,615,875	239,400	1,198,500	2,233,600	9,408,900
1995	1,286,400	1,959,975	127,800	374,400	1,510,600	5,414,600
1996	1,429,900	2,597,650	175,800	910,400	738,200	6,901,740
1997	1,872,100	2,368,310	123,300	657,000	2,710,800	4,420,700
1998	2,580,600	2,447,570	367,580	938,400	2,224,200	5,720,136
1999	1,720,700	2,469,000	223,400	664,400	1,989,300	3,282,090
2000	1,623,700	2,043,225	498,500	14,400	7,200	
2001	14,400	25,200	14,400	14,400	7,200	

ever, why the mean distance moved by lake trout tagged in MI-5 was higher during the spawning season than the nonspawning season. Movement of lake trout tagged during the spawning season and recaptured during the nonspawning season should be least affected by homing behavior and therefore is the most appropriate for use in modeling lake trout movements.

Movement among Management Units

We found that lake trout did not emigrate at equal rates to other areas of Lake Superior, which agrees with some studies of lake trout movement in Lake Superior (Pycha et al. 1965 for fish tagged in MI-4; Eschmeyer et al. 1953 for fish tagged in WI-2), but disagrees with others (Pycha et al. 1965 and Swanson 1973 for fish tagged in WI-2). For example, our finding that lake trout tended to stay in MI-4 agrees with that of Pycha et al. (1965), who reported that most hatchery-reared lake trout remained in MI-4 and that more fish emigrated to the east than to the west. In contrast, Eschmeyer et al. (1953) found that most wild-born lake trout tagged in MI-4 were recaptured in MI-4 but that more fish emigrated to the west than to the east. However, the small sample size (24 recaptures) observed by Eschmeyer et al. (1953) and the fact that Pycha et al. (1965) and Eschmeyer et al. (1953) did not account for spatial and temporal differences in recapture effort between management units make direct comparisons between our results and theirs tenuous. Furthermore, demographic changes in lake trout populations (hatchery-reared dominance to wild-born dominance) and

TABLE 4.—Mean distance moved (km), as determined by one-way ANOVA, for lake trout tagged in six management units of Lake Superior during 1973–2001 and recaptured during the nonspawning season (December–September). The standard deviation (SD), upper and lower 95% confidence limits about the mean (UCL, LCL), 90th percentile ($p_{0.90}$) for distance moved, and degrees of freedom (df) are given. Lake trout were recaptured in gill-net and angling fisheries.

Statistic	Tagged population All	WI-1	WI-2	MI-2	MI-3	MI-4	MI-5
Mean	42.02	62.71	44.28	60.85	66.02	28.30	44.16
SD	48.76	79.92	54.83	38.36	49.59	35.30	40.30
UCL	45.22	88.46	50.32	70.04	77.40	32.07	54.45
LCL	38.82	36.96	38.24	51.67	54.65	24.54	33.88
$p_{0.90}$	82.88	196.61	79.48	94.16	110.42	54.18	79.10
df	889	36	316	66	72	336	58

TABLE 5.—Mean distance moved (km), as determined by one-way ANOVA, for lake trout tagged in four management units of Lake Superior during 1973–2001 and recaptured during the spawning season (October or November). The standard deviation (SD), upper and lower 95% confidence limits about the mean (UCL, LCL), 90th percentile ($p_{0.90}$) for distance moved, and degrees of freedom (df) are given. Lake trout were recaptured in gill-net and angling fisheries.

Statistic	Tagged population				
	All	WI-2	MI-3	MI-4	MI-5
Mean	17.37	9.46	25.46	13.96	81.08
SD	37.82	26.22	43.36	26.06	74.59
UCL	20.55	12.52	34.67	18.23	106.93
LCL	14.19	6.41	16.24	9.68	55.24
$p_{0.90}$	41.79	31.83	50.11	41.79	167.88
df	542	282	84	142	31

ecological changes (reflected by changes in the prey base from rainbow smelt *Osmerus mordax* dominance to cisco *Coregonus artedi* dominance) in Lake Superior between the study periods of Pycha et al. (1965) and Eschmeyer (1953) and our study may confound comparisons of movement. Our finding that lake trout tagged in WI-2 emigrated more to the west than to the east is similar to that of Eschmeyer et al. (1953), who found similar movement patterns for wild-born lake trout tagged in WI-2 during 1951. Our results and those of Eschmeyer et al. (1953), however, contradict those of Pycha et al. (1965) and Swanson (1973), who found that hatchery-reared and wild-born lake trout tagged in WI-2 moved east. Swanson (1973) attributed the difference between his results and those of Eschmeyer et al. (1953) to the location of the tagging site in relation to prevailing surface currents. Swanson (1973) concluded that lake trout tagged in the western end of WI-2 were likely to be caught in the counterclockwise eddy current located in the western end of the lake, while lake trout tagged in the eastern portion of WI-2 were likely to be influenced by easterly flowing surface currents and subsequently recaptured in Michigan waters. Our findings do not agree with this explanation because most lake trout in our study were tagged in the eastern portion of WI-2, at or adjacent to the tagging location used by Swanson (1973), and our results indicated that westward movement was more common than eastward movement. The discrepancy in emigration patterns between these two studies probably occurred because our analysis accounted for spatial and temporal variability in recapture effort, but the analysis by Swanson (1973) did not.

Factors Associated with Movement Distance

Our findings suggest that movement distance of lake trout was unrelated to body length, which is inconsistent with the results of previous studies (Eschmeyer et al. 1953; Peck 1981). For example, Eschmeyer et al. (1953) found that large lake trout moved greater distances than small lake trout during the first year after being tagged in MI-4 and WI-2. Similarly, Peck (1981) found that large lake trout fry moved greater distances from an artificial spawning reef than did small fry. The lake trout studied by Eschmeyer et al. (1953) ranged from 229 to 785 mm in total length, and the lake trout fry studied by Peck (1981) ranged from 25 mm on 10–11 May to 45 mm on 26–27 July. The fact that our data set did not include lake trout as small as these may explain why the relation between body length and distance moved was not apparent in our analysis.

Our results suggest that movement distances of lake trout tagged in WI-1 and WI-2 are not related to fish age, which disagrees with other studies that have reported further movement by mature lake trout than immature lake trout (Pycha et al. 1965;

TABLE 6.—Mean distance moved (km), as determined by one-way ANOVA, for lake trout tagged in four management units of Lake Superior during 1973–2001 and recaptured during the spawning (October–November) and nonspawning (December–September) seasons. Lower and upper 95% confidence limits (CL) about the mean are given in parentheses, and the degrees of freedom (df) are given. Lake trout were recaptured in angling and gill-net fisheries.

Season and statistic	Management unit			
	WI-2	MI-3	MI-4	MI-5
Spawning				
Mean	9.46	25.46	13.96	81.08
CL	(6.41, 12.52)	(16.24, 34.67)	(9.68, 18.23)	(55.24, 106.93)
Nonspawning				
Mean	44.28	66.02	28.30	44.16
CL	(38.24, 50.32)	(54.65, 77.40)	(24.54, 32.07)	(33.88, 54.45)
df	599	157	479	90

TABLE 7.—Mean percentage of tagged lake trout recaptured in management units in U.S. waters of Lake Superior for each management unit where tagging occurred. Percentages were calculated separately for gill-net and angling fisheries based on mark–recapture data from 1973, 1976, and 1980–2001, and then averaged except for fish tagged in MI-3 (gill-net recaptures only). Lower and upper 95% confidence limits are given in parentheses. Numbers of lake trout tagged (Nt) and recaptured (Nr) in each tagging unit are given.

Variable/ recapture unit	Tagging unit					
	WI-1	WI-2	MI-2	MI-3	MI-4	MI-5
Nt	5,348	28,604	4,233	714	3,644	2,097
Nr	37	317	67	66	337	59
MN-1	11.2 (−2.1, 24.5)	5.0 (4.6, 5.4)	0.0	0.0	0.0	0.0
MN-2	0.0	0.0	0.0	0.0	0.0	0.0
MN-3	0.0	2.7 (0.0, 5.4)	1.8 (−1.8, 5.4)	0.0	1.0 (−0.9, 2.9)	0.0
WI-1	63.0 (42.2, 83.7)	47.1 (18.2, 75.9)	1.1 (−1.1, 3.3)	0.0	0.0	0.0
WI-2	14.7 (−2.1, 31.5)	26.2 (17.6, 34.9)	6.3 (4.3, 8.2)	3.1	2.3 (−1.7, 6.3)	0.2 (−0.2, 0.5)
MI-1	0.0	0.0	0.0	0.0	6.7 (−6.5, 19.9)	0.0
MI-2	4.4 (−4.3, 13.1)	10.8 (1.2, 20.4)	78.7 (64.9, 92.5)	16.9	0.5 (−0.5, 1.5)	0.7 (−0.7, 2.1)
MI-3	0.6 (−0.6, 1.9)	1.0 (−1.0, 2.9)	8.9 (−8.6, 26.4)	42.2	3.7 (−3.6, 11.1)	2.4 (−2.3, 7.1)
MI-4	0.5 (−0.5, 1.5)	6.5 (−2.3, 15.4)	0.9 (−0.9, 2.7)	11.1	61.5 (44.2, 78.8)	25.5 (3.2, 47.8)
MI-5	5.5 (−5.3, 16.3)	0.7 (−0.7, 2.1)	1.7 (−1.6, 4.9)	26.7	21.0 (20.0, 22.0)	70.3 (51.4, 89.1)
MI-6	0.0	0.0	0.6 (−0.5, 1.6)	0.0	1.3 (−1.3, 3.9)	0.5 (−0.5, 1.6)
MI-7	0.0	0.0	0.0	0.0	1.9 (−1.1, 4.9)	0.5 (−0.4, 1.4)

Lawrie and Rahrer 1973). For example, Pycha et al. (1965) suggested that mature lake trout dispersed more widely than immature lake trout. Similarly, Lawrie and Rahrer (1973) suggested that lake trout movement distance differed between mature and immature fish. In our analysis, most (95%) recaptured lake trout originally tagged in WI-1 and WI-2 were age 7 or greater, so our analysis may have lacked enough immature lake trout to determine whether movement of mature and immature lake trout differed.

We found that movement of lake trout varied with time at liberty for one of six tagged populations tested, which is consistent with other studies of lake trout in Lake Superior (Eschmeyer et al. 1953; Buettner 1961). Our results suggest that distance moved by lake trout tagged in MI-4 was positively related to time at liberty, which agrees with studies by Eschmeyer et al. (1953) for lake trout tagged in WI-2 and Buettner (1961) for those tagged in MN-3, WI-2, MI-5, and MI-8. The relation between time at liberty and distance moved may be weak or difficult to detect because (1) most lake trout tagged on spawning reefs, as in our study, return to the same spawning reef and are therefore likely to be recaptured near the tagging location, or (2) most lake trout tend to remain near release locations regardless of how long they are at liberty (Eschmeyer et al. 1953; Buettner 1961).

TABLE 8.—Effects of length (*L*), age (*A*), time at liberty (*T*), sex (*S*), and origin (*O*) on distance moved by recaptured lake trout in six management units of Lake Superior during 1973–2001.

Management unit	Model covariate	*F*-ratio	df	*P*
WI-1	*L*	2.5333	1,25	0.12403
	A	2.4172	1,25	0.13258
	T	1.5256	1,25	0.22826
	S	3.1065	1,25	0.09020
	O	0.0209	1,25	0.88619
WI-2	*L*	1.8081	1,195	0.18029
	A	0.2771	1,195	0.59923
	T	0.0515	1,195	0.82079
	S	2.2188	1,195	0.13795
	O	0.1835	1,195	0.66882
MI-2	*T*	0.0044	1,65	0.94707
MI-3	*T*	0.4485	1,71	0.50522
MI-4	*L*	0.1569	1,34	0.69452
	T	5.6219	1,34	0.02355
	O	3.3669	1,34	0.07528
MI-5	*T*	0.1834	1,57	0.67010

We expected to find differing movement distances between wild-born and hatchery-reared lake trout because hatchery-reared lake trout are less likely than wild-born lake trout to return to the same spawning reef (Swanson 1973; MacLean et al. 1981; Krueger et al. 1986). This apparent wandering by hatchery-reared lake trout reduces their likelihood of recapture at a spawning (tagging) site, thereby causing their movement distance to appear greater than that of wild-born lake trout. The lack of relation between origin and distance moved for two of our three tagged populations may be attributable to small sample sizes. Of the 201 tag–recapture records we analyzed from WI-2, 41 were wild-born and 160 were hatchery-reared lake trout; in contrast, we had only 34 recaptures from lake trout tagged in WI-1 (5 wild-born, 26 hatchery-

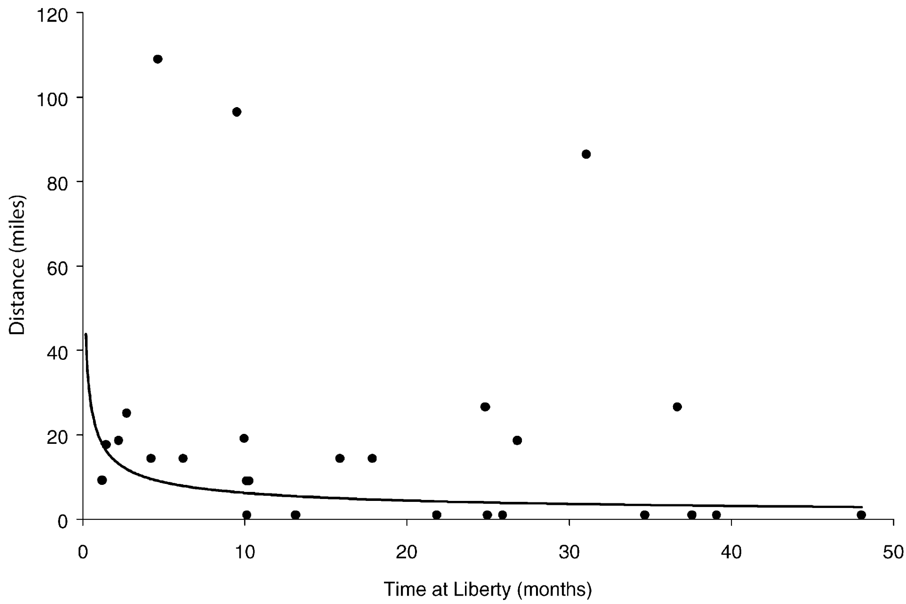

FIGURE 2.—Distance moved (D_i; 1 mi = 1.61 km) versus time at liberty (T_i) for recaptured lake trout that were tagged in U.S. management unit MI-4 of Lake Superior during 1983–2000. The curve is described by the equation, $D_i = e_i^{2.968798788} \cdot T_i^{-0.49451504}$. Lake trout were recaptured in gill-net and angling fisheries.

reared) and 38 from those tagged in MI-4 (33 wild-born, 5 hatchery-reared). Our findings would be stronger if at least 30 recaptures of each origin had been attained from lake trout tagged in each management unit.

We expected to find a difference in movement distance between male and female lake trout because males spend more time at spawning reefs and are therefore more likely to be recaptured near the tagging area, thereby appearing to move less than females (Eschmeyer 1955; MacLean et al. 1981). For example, Eschmeyer (1955) found that male lake trout remained on or near spawning grounds for several weeks during the spawning season, and MacLean et al. (1981) found that female lake trout moved further than males. Our results from two tagged populations (WI-1–2), however, did not support our expectation. Of the 201 tag–recapture records for WI-2, 154 were males and 47 were females, so the lack of apparent difference in movement distance between males and females in WI-2 was not caused by low sample sizes. In contrast, of the 31 tag–recapture records for WI-1, 23 were males and 8 were females, so low sample sizes may have prevented us from detecting movement differences.

Our study of lake trout movement in Lake Superior could have been improved if recapture sample sizes were larger. In most areas of Lake Superior (e.g., MI-1, MI-6–8, MN-1–3, and Canadian waters), extensive tagging programs would need to be enacted before mean distance moved, percent movement, or factors influencing movement distances could be quantified with greater certainty than was permitted in our study. For WI-2, where a large tagging program already exists, incomplete records prevented analysis of a large number of recaptures. Recapture records from agency surveys were more complete than records from recreational, tribal, or commercial fisheries, but the latter three fisheries tend to be more spatially and temporally dispersed. Fishery agencies around the lake should therefore either reward the reporting of tag recaptures or promote the importance of such reporting to recreational, tribal, and commercial fishers to increase the number of recapture records that are useful for movement analyses. The sex of live lake trout can be difficult to determine at times other than the spawning season, but body length, origin, and date of capture can be recorded for every lake trout recaptured in survey nets. Ages should be estimated for all recaptured lake trout that cannot be released. Agencies around Lake Superior should attempt to extract the maximum amount of information from each recaptured lake trout so that mean distance moved and percent movement can be estimated for fish tagged in all management units and so that factors influencing movements can be more thoroughly evaluated.

Management Implications

Our findings permit fishery managers to account for movement among management units in catch-at-age models for lake trout in Lake Superior. Because lake trout movements in the lake had not previously been quantified, fishery managers that use catch-at-age models to estimate sustainable harvest levels of lake trout in Lake Superior have assumed that lake trout move at equal rates among management units. This assumption could lead to overfishing if harvest levels are set too high because movement patterns are not quantified. In addition, rates of lake trout immigration may confound estimation of recruitment rates (Hansen et al. 1996). Lake trout that move across jurisdictional boundaries may be subjected to different levels of fishing pressure and exploitation in each jurisdiction because of variation in fishery regulations (Hansen et al. 1995). Our results indicate that on average, lake trout tagged in WI-1–2 and MI-2–5 and recaptured during the nonspawning season moved approximately 42 km while at large. If lake trout spawn within 42 km of a jurisdictional boundary between two adjacent management units, fishery biologists can assume that spawners will move across the boundary between spawning events, and may wish to model such border populations under one catch-at-age model. Catch-at-age models used to estimate harvest levels in WI-1–2 and MI-2–5 can incorporate our estimates of percent movement between management units, and fishery managers can predict the distance moved by lake trout in MI-4 based on our model for time at liberty.

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