

Lake Trout Movements in Northwestern Lake Michigan

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Abstract.—We quantified the distance that lake trout *Salvelinus namaycush* moved in northwestern Lake Michigan and examined (1) the directional preference and (2) the effect of population density on movement. Lake trout were captured in spring and fall 1983–1996, tagged with Floy anchor tags, and recaptured during subsequent agency sampling and by commercial fishers and anglers during 1983–1997. Angler recaptures were used to quantify movements; these recaptures were standardized to 10,000 salmonid angler-hours (giving recaptures per effort [RPE]) to account for the spatial and temporal variation in recapture effort. Movement was inferred from the spatial and temporal differences in the distribution of RPE. The dispersal radius, an index of the area occupied by tagged lake trout, was defined as the area containing 90% of the total RPE. It was estimated by fitting the cumulative proportion of RPE versus distance from the tagging location to an exponential sigmoid model and using inverse prediction. We used linear regression to test for density dependence in movement. Lake trout tagged in spring occupied a larger area than those tagged in fall and increased their range as population density increased. Directional movement differed for spring- and fall-tagged fish. Spring-tagged fish showed no directional tendencies in movement, but fall-tagged fish tended to move more to the south than to the north. There was no significant difference in directional movement between recapture seasons. Our results will be useful for the management and restoration of lake trout in Lake Michigan by providing information that can be incorporated into population models and management decisions about refuges and management zones within the lake.

Fisheries management includes understanding, assessing, and managing fish populations as well as human users of the resource and fish habitat (Krueger and Decker 1999; Nielsen 1999). Fish movement may affect all aspects of fisheries management. Movement may influence fish population dynamics by the addition or subtraction of members of a population, by altering species interactions, or by altering the ability of a population to maintain genetic diversity (Turchin 1999). As estimates of the abundance of commercially exploited species may be strongly influenced by move-

ment patterns, understanding the spatial dynamics of fish populations is critical to assessing and managing fisheries (Pelletier and Parma 1994). For example, Atlantic herring *Clupea harengus* are now managed and exploited as unit stocks based on knowledge of their movements and habitat use during the spawning season (Wheeler and Winters 1984).

Movement may also affect the management of lake trout *Salvelinus namaycush* in the Great Lakes. Lake trout were an important native predator in all the Laurentian Great Lakes and were commercially important in many areas before their populations collapsed during the 1940s and 1950s (Hartman 1988; Elrod et al. 1995; Eschenroder et al. 1995; Hansen et al. 1995; Holey et al. 1995). Lake Michigan sustained lake trout yields of 1.8–4.5 million kg annually from 1889 to 1944, but yield declined 95% by 1949 and was only 15 kg in 1955 (Hile et al. 1951; Eschmeyer 1957; Wells

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and McLain 1973; Holey et al. 1995; Hansen 1999). Chemical control of sea lampreys since 1960, closure of the commercial lake trout fishery in 1965, and clean water legislation in the 1960s facilitated lake trout restoration in Lake Michigan (Smith and Tibbles 1980; Holey et al. 1995). Stocking of hatchery-reared lake trout, begun in 1965, rebuilt substantial stocks of adult lake trout throughout Lake Michigan (Hartman 1988; Holey et al. 1995). Increased abundance fueled a recreational fishery for lake trout in Lake Michigan, with the harvest from Wisconsin waters increasing from 622 in 1969 to over 113,000 in 1987 (Hansen et al. 1991; B. Eggold, Wisconsin Department of Natural Resources, personal communication). However, rehabilitation efforts have yet to reestablish self-sustaining lake trout populations, so the sport and tribal commercial fisheries are sustained by stocking (Holey et al. 1995).

Since stocking is presently the only source of recruitment to lake trout populations in Lake Michigan, knowledge of the area that lake trout occupy can help in choosing stocking locations or the distances between stocking sites. More specifically, knowing this area and the tendency of fish to leave, enter, and return to it may be useful in defining management zones and potential refuge sizes and locations, as well as in evaluating the effectiveness of existing refuges. Management of contaminants in Lake Michigan also relies on an understanding of lake trout movements. Lake trout bioaccumulate organic contaminants such as dichloro-diphenyl-trichloroethane (DDT) and polychlorinated biphenyls (PCBs), which pose potential health hazards to humans who consume contaminated fish (Delfino 1979; Sonzogni and Swain 1980; Rodgers and Swain 1983; Jacobson and Jacobson 1993). Contaminants have also been shown to hinder lake trout reproduction by increasing egg and fry mortality (Berlin et al. 1981; Mac et al. 1993). Lake trout are a vector of transport for contaminants, and knowledge of lake trout movements can be useful in understanding contaminant dynamics, such as in the Lake Michigan Mass Balance (LMMB) project, which was started in 1994 by the U.S. Environmental Protection Agency (EPA 1997).

Our objectives were to (1) quantify movement distance, (2) test for directional preference, (3) determine the extent to which lake trout return to the tagging area, (4) test for seasonal differences in movement, and (5) test for any effects of density on movement. We used data on adult lake trout that were tagged in northwestern Lake Michigan

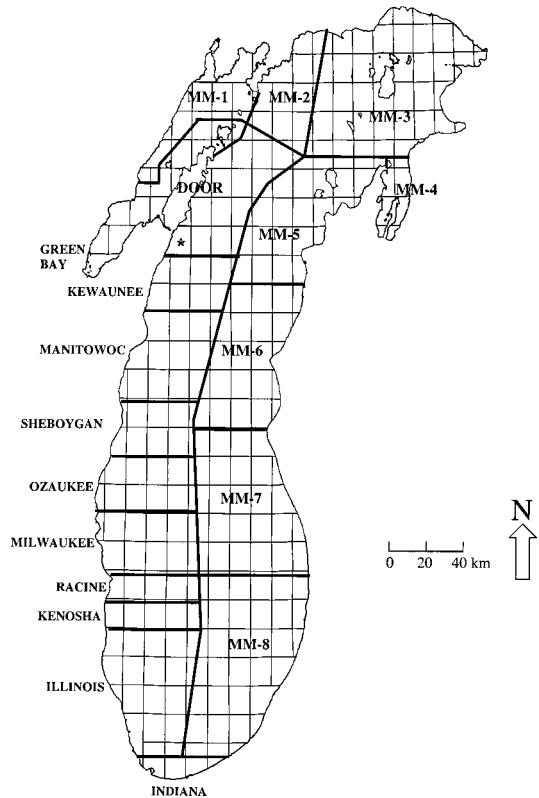


FIGURE 1.—Map of Lake Michigan showing the grids used to describe lake trout recapture locations and the spatial units used to describe angler effort (i.e., county, statistical district, or state). The star shows the approximate tagging location.

during 1983–1997 to address these questions. Based on previous studies of lake trout movements in Lake Michigan (Smith and Van Oosten 1939; Rybicki and Keller 1978) and Lake Superior (Eschmeyer et al. 1953; Buettner 1961; Rahrer 1968; Pycha 1973; Swanson 1973; Hansen et al. 1995), we hypothesized that lake trout would generally occupy an area within 80 km of the tagging location. We also believed that these fish would return to distinct locations to spawn in successive years, as they have been shown to do in Lake Superior (Rahrer 1968; Swanson 1973). Finally, we hypothesized that lake trout movement would increase as population density increased.

Methods

Study area.—Field sampling was conducted in the Clay Banks area of northwestern Lake Michigan, which is located off the eastern shore of the Door County peninsula between Algoma, Wisconsin, and the Sturgeon Bay ship canal (Figure 1).

The Clay Banks area contains several reefs where lake trout spawned historically (Coberly and Horrall 1980). The substrate at these reefs is made up mostly of rubble (Edsall et al. 1995). During 1986–1995, a triangular-shaped refuge existed in the Clay Banks area, within which lake trout fishing was prohibited (Holey et al. 1995).

Lake trout capture, tagging, and recapture.—Lake trout were captured with gill and pound nets during 1983–1996. During 1983–1989 and 1991–1993, spawning lake trout were captured in multifilament nylon gill nets set overnight at depths of 6–14 m. Gill-net sampling was conducted from late October to early November of each year. During 1983–1988, gill nets consisted of eight 30.5-m × 2-m panels of stretched mesh (64, 76, 89, 102, 114, 127, 140, and 152 mm, respectively). In 1988, additional gill nets consisting of four 76.2-m × 2-m panels of stretched mesh (114, 127, 140, and 152 mm) were used. During 1989 and 1991–1993, only gill nets of the latter type were fished. During spring 1984–1990 and 1992–1996, lake trout were sampled with a pound net. Pound-net sampling was conducted from early May to late June of each year. The pound net extended from the lake bottom to the surface (10 m), the pot measured 12 m square and 10 m deep, and the lead was 355-mm stretched mesh that extended 457 m toward shore. No lake trout were tagged in fall 1990 or spring 1991.

Lake trout captured in both gears were measured to the nearest millimeter (total length) and examined for missing fins (since all lake trout in Lake Michigan are hatchery fish, they are marked by the removal of one or more fins, based on the year stocked) and the presence of tags. For recaptures of tagged fish, tag identification numbers were recorded and the fish were released. For lake trout without tags, an anchor tag was secured near the middle and base of the dorsal fin prior to release. Anchor tags were either Floy FD-67C tags, which consisted of an anchor and a vinyl tube bearing an identification number and return address, or Floy FD-68BC tags, which also had a plastic bead on the distal end of the tube to prevent the tube from coming off the anchor. Over the study period, 67,119 lake trout were tagged, 11,681 after capture in gill nets and 55,438 after capture in pound nets.

Tagged lake trout were recaptured during subsequent Lake Michigan management agencies' sampling efforts and by commercial and sport fishers during 1983–1997. Altogether, 8,905 lake trout were recaptured, 7,806 of which were spring-tagged fish and 1,099 fall-tagged fish. Agency as-

sessments accounted for 4,168 of the recaptures (3,558 spring-tagged and 610 fall-tagged). Sport anglers recaptured 3,400 lake trout (3,017 spring-tagged and 383 fall-tagged). Commercial fishers recaptured 1,337 lake trout (1,231 spring-tagged and 106 fall-tagged). The number of recaptures in a given area at a given time is a function not only of the number of tagged fish present but also of the amount of fishing effort exerted in the area at that time (Hilborn 1990). Sportfishing effort provided the most consistent source of recapture effort, both spatially and temporally, around Lake Michigan (Figures 2, 3); therefore, only lake trout recaptured by sport fishers were used to quantify the distance and direction of lake trout movements. Tags from angler-recaptured lake trout were returned voluntarily.

The location of each recapture was reported to the nearest 10' × 10' latitude–longitude grid cell. With the exception of grids that adjoined land, grid cells were 207 km² (Figure 1). For each lake trout recapture, the distance moved was calculated and the direction (north, south, or east) assigned. Distance moved was computed as the distance from the center of the tagging grid to the center of the recapture grid, measured to the nearest 16 km. Since lake trout were tagged in two separate assessments at different times of the year, spring-tagged and fall-tagged fish were treated as separate populations in all analyses. This allowed us to compare movements by these two different groups. Although we did not necessarily believe that spring- and fall-tagged fish represented completely different stocks, we felt that the two groups might be using an area for different reasons (i.e., spawning in the fall and foraging in the spring) and that they might exhibit differences in movement.

Data standardization.—To account for spatial and temporal heterogeneity in recapture effort (angling effort), recaptures were standardized as the number per 10,000 salmonid angler-hours (RPE; Hilborn 1990; Sheridan and Castro Melendez 1990). Estimates of angling effort by ramp and charter fishers targeted at salmonids were obtained from annual creel surveys conducted by the states of Wisconsin, Michigan, and Illinois (Absher and Collins 1987; Hansen et al. 1991; Eggold 1996; Lockwood 1997). Angling effort (angler-hours) in Wisconsin waters was estimated for each county and month from March through November (sometimes 2 months, i.e., March and April, September and October, and November and December, were combined). Angling effort from Michigan waters was estimated for each statistical district and

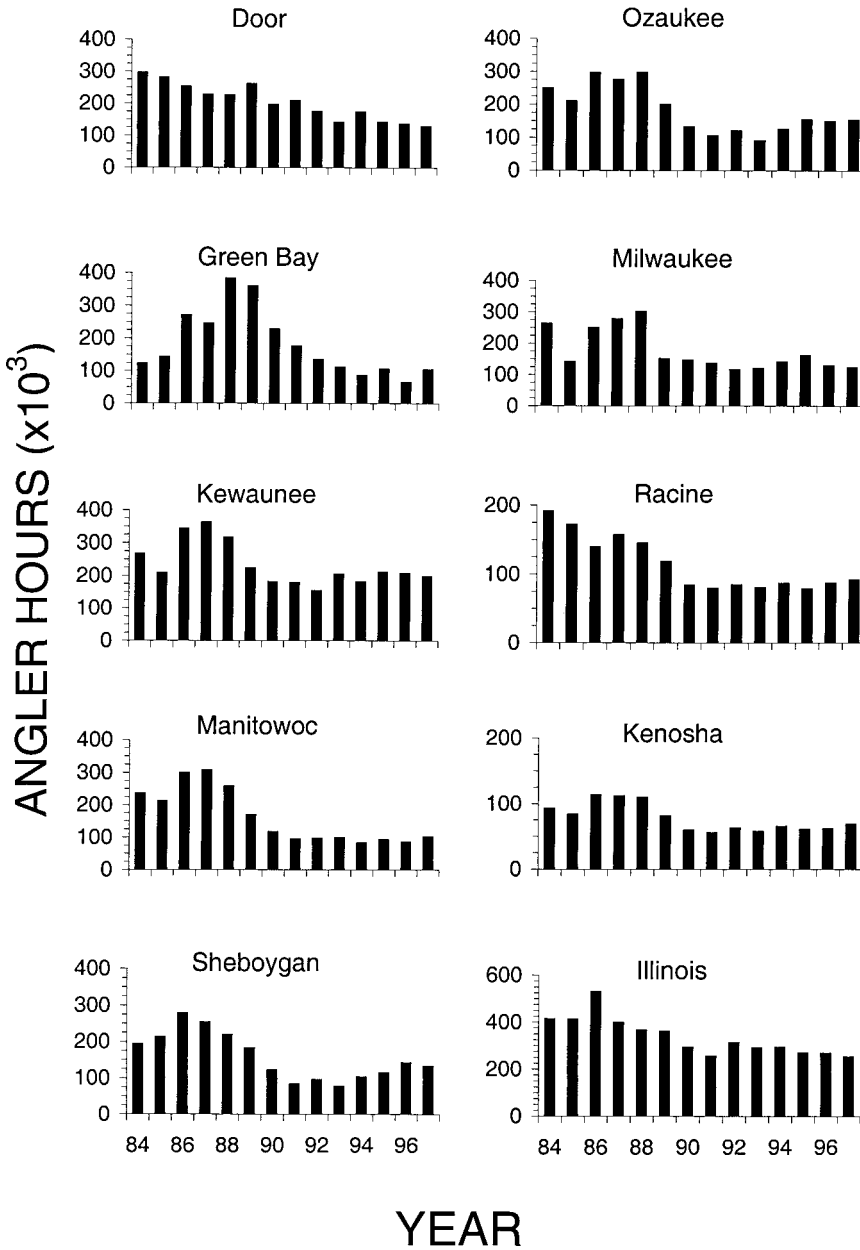


FIGURE 2.—Salmonid angling effort (h) for Wisconsin and Illinois waters of Lake Michigan during 1984–1997. Wisconsin waters are divided into counties.

month from April through November. Statistical districts consist of several grids and are used to summarize fishery information in the Great Lakes (Smith et al. 1961). Angling effort in Illinois waters was estimated for all state waters each month from April through September.

Lake trout recaptures were summed for all grids within the spatial unit for which angling

effort was estimated (i.e., county, statistical district, or state). Recaptures from Wisconsin waters were summed for all grids within each county that borders Lake Michigan; counties consisted of 5–13 grids. For Michigan waters, recaptures were summed by statistical district; these districts consisted of 6–41 grids. All recaptures from Illinois waters (18 grids) were combined. Annual RPE

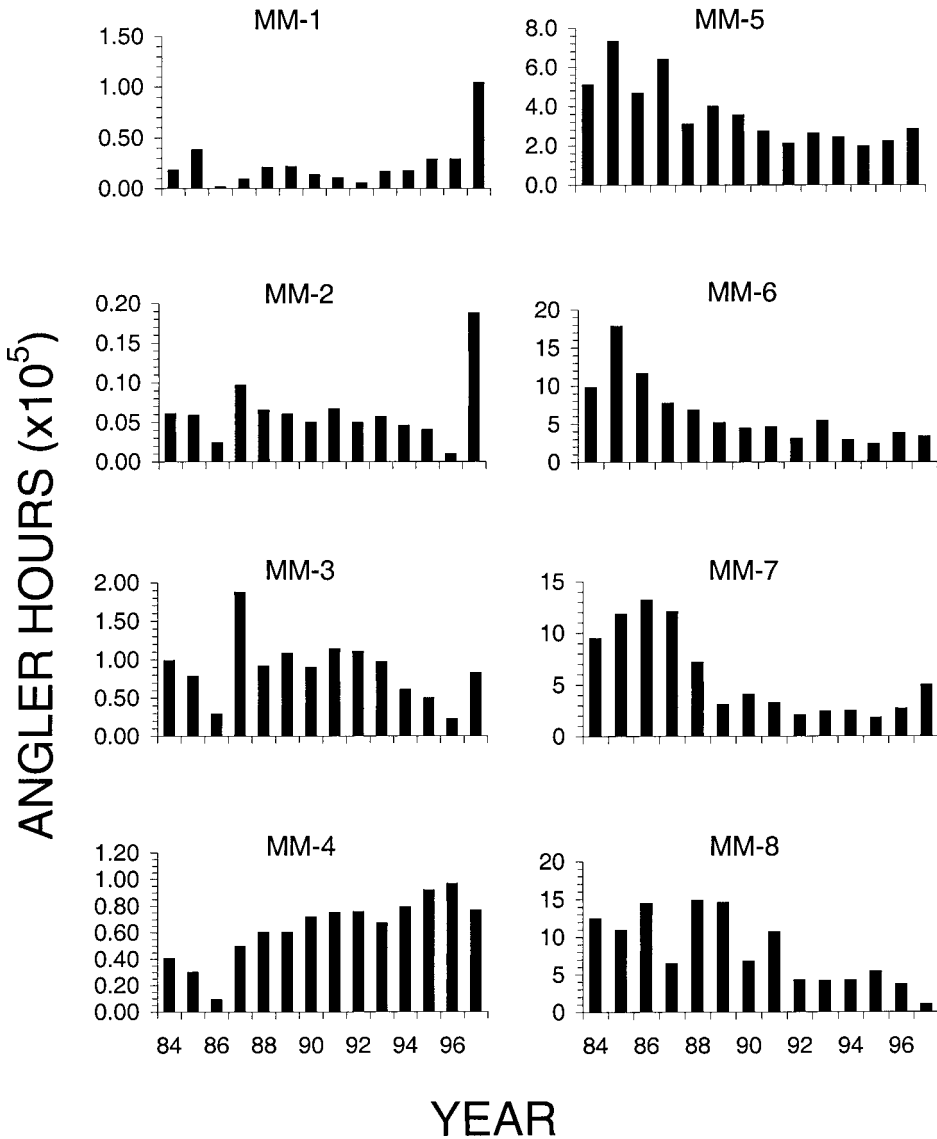


FIGURE 3.—Salmonid angling effort (h) for Michigan waters of Lake Michigan during 1984–1997, by statistical district.

was calculated by dividing the recaptures within each spatial unit by the angling effort estimated for that unit in that year and multiplying by 10,000. Seasonal RPE was calculated by combining recaptures and effort by season (spring, summer, or fall). Spring included March–May, summer June–August, and fall September–November. All years were combined in seasonal estimates. Movement distance associated with the RPE estimates was measured (to the nearest 16 km) from the center of the tagging grid to the

center of the spatial unit of angling effort (Figures 1, 2, 3).

Movement distance.—Movement distance was quantified by dispersal radius. The dispersal radius was an index of the area occupied by lake trout that is analogous to their home range. Home range is often defined as the area in which an animal tends to stay (Clarke 1954) and quantified as the area within which an animal spends 90% of its time (Tufto et al. 1996). Home range generally considers individual animals, whereas we

were concerned with the movements of large groups of fish. Thus, we defined the dispersal radius as the straight-line distance from the tagging location within which 90% of the total RPE occurred.

To calculate dispersal radius, we needed to calculate the cumulative proportion of total RPE as a function of dispersal distance. Therefore, we fitted an exponential sigmoid model,

$$y = \frac{\alpha}{(1 + \beta e^{Kx})},$$

which describes the cumulative proportion of RPE (y) as a function of dispersal distance (x). In this three-parameter model, α is the maximum proportional RPE that can be obtained, β is a unitless constant that scales the curve according to the proportion of RPE at a distance of zero, and K is the rate (proportional RPE per kilometer) at which the proportional RPE increases with distance. The parameters were estimated numerically using a Gauss–Newton search algorithm that relied on exact derivatives (SPSS 1997). Separate models were fitted for each recapture season (for all years combined) and year (for all recapture seasons combined).

Inverse prediction was used to estimate the distance ($x_{0.90}$) at which the cumulative proportion of total RPE was equal to 0.90 using the estimated parameters from the nonlinear regression above (Neter et al. 1996):

$$x_{.90} = \frac{\log_e[(\alpha/0.90) - 1] - \log_e\beta}{K}.$$

Dispersal radii were estimated by tagging season (fall and spring) for each recapture season (spring, summer, and fall). Two-factor analysis of variance (ANOVA) without replication (Zar 1999) was used to compare the effect of tagging and recapture seasons (factors) on dispersal radius (the dependent variable).

Tagging-site fidelity.—There has been interest in determining whether or not lake trout display homing tendencies (Horrall 1981). Wheeler and Winters (1984) determined the extent of Atlantic herring homing by examining tag recoveries made in successive years at the same spawning areas. They noted that although homing was defined as returning to the natal spawning ground to spawn it was not possible to determine whether the returning herring were born at those locations. We quantified the extent to which lake trout returned to the tagging location, which we defined as tagging-site

fidelity. This was based on the definition of fidelity as the degree of faithfulness to a location (Hanson 1962). In our study, we could not determine whether the lake trout that were recaptured in or with the same gear and in the same location in a subsequent year had actually left the area. We calculated tagging-site fidelity as the ratio of the number of lake trout that were tagged during a tagging event and recaptured during a subsequent tagging event (at the same location) to the total number of lake trout recaptured anywhere during that time period (i.e., spring for pound-net recaptures and fall for gill-net recaptures). We calculated this index for both fall- and spring-tagged fish. For fall-tagged (spawning) lake trout, tagging-site fidelity provides a measure analogous to homing, in that fish displayed fidelity to a specific spawning area. For spring-tagged fish it indicates the degree to which lake trout remain in the same area for other reasons, such as foraging.

Directional movement.—We tested for differences in the direction of lake trout movements by examining the spatial distribution of RPE with respect to the tagging location. We used a three-way ANOVA without replication to test the effect of tagging season (spring and fall), recapture season (spring, summer, and fall), and direction (north and south) on RPE (Zar 1999). We used paired-sample t -tests to test the null hypothesis that RPE was the same for north and south (Sheridan and Castro Melendez 1990; Zar 1999). We did separate t -tests for spring-tagged and fall-tagged fish. Lake trout recaptured in the waters of Green Bay and Door County, Wisconsin, and in Michigan statistical districts MM-1 and MM-2 (Figure 1) were included in the calculation of RPE to the north of the tagging site. Lake trout recaptured in Kewaunee, Manitowoc, Sheboygan, Ozaukee, Milwaukee, Racine, and Kenosha counties and in Illinois waters were included in the calculation of RPE to the south of the tagging location. Lake trout recaptured in statistical districts MM-3 to MM-8 were considered to be east of the tagging location. As only nine recaptures were made to the east of the tagging location during the entire study period, these fish were not included in the directional analyses. RPE was calculated by summing recaptures and salmonid angling effort for each direction and year. Seasonal RPE values were calculated by summing recaptures and salmonid angling effort by season (for all years) and direction.

Density dependence.—The effect of adult lake trout population density in the Clay Banks area on movement was tested by means of linear regres-

TABLE 1.—Parameter estimates for the exponential sigmoid models (asymptotic standard errors in parentheses) and estimates of the dispersal radius for spring- and fall-tagged lake trout from northwestern Lake Michigan in three recapture seasons during 1983–1997. Dispersal radius is defined as the distance from the tagging location within which 90% of recaptures per effort were made. Parameter estimates were based on a nonlinear regression using miles as the distance unit; kilometers were calculated by multiplying the dispersal radius in miles by 1.609344.

Recapture season	α	β	κ	R^2	Dispersal radius (km)
Spring-tagged fish					
Spring	0.98594 (0.01195)	4.69626 (0.81938)	-0.09174 (0.00875)	0.992	68.4
Summer	1.00192 (0.03069)	15.6787 (12.1697)	-0.12086 (0.03425)	0.959	65.6
Fall	1.00874 (0.02602)	2.97431 (0.84675)	-0.07640 (0.01487)	0.960	67.4
Fall-tagged fish					
Spring	1.00331 (0.00689)	15.4779 (3.50811)	-0.13798 (0.01111)	0.998	57.1
Summer	0.99240 (0.02398)	123.244 (181.8616)	-0.19554 (0.07026)	0.978	58.4
Fall	0.99657 (0.01567)	26.4235 (15.1993)	-0.14577 (0.02697)	0.990	60.8

sion analysis. Annual estimates of dispersal radius (the dependent variable) calculated from total annual recaptures and angling effort were regressed on population density indexed by spring pound-net catch per effort (CPE; number/50 nights). We used spring pound-net CPE to index population density because it was the only spring assessment conducted during the entire study period and there has been some question about the validity of using fall gill-net CPE as an index of population density (Holey et al. 1995). We considered a positive slope that was significantly different from zero ($P \leq 0.05$) as indicating density dependence.

Results

Movement Distance

Dispersal radii were higher for spring-tagged than for fall-tagged lake trout but were not significantly different among recapture seasons. Spring-tagged lake trout occupied an area 65.6–68.4 km from the tagging location and fall-tagged lake trout an area 57.1–60.8 km from the tagging location, depending on recapture season (Table 1). Dispersal radii were significantly larger for spring- than for fall-tagged fish ($F = 36.11$; $df = 1, 2$; $P \leq 0.03$) but did not differ among recapture seasons ($F = 0.80$; $df = 2, 2$; $P = 0.55$).

Tagging-Site Fidelity

The tendency for lake trout tagged in northwestern Lake Michigan to be recaptured at the location where they were tagged was similar for both spring- and fall-tagged fish. Over 74% (283

out of 382) of fall-tagged lake trout recaptured in fall were recaptured where they were tagged in an earlier year. The same was true for lake trout tagged in spring; nearly 73% (1,298 out of 1,783) of all spring recaptures were made in the location where the fish were tagged in an earlier year.

Directional Movement

Directional preference differed between spring- and fall-tagged lake trout but not for fish recaptured in the different seasons (Figure 4). Recapture season had no significant effect on RPE ($F = 0.922$; $df = 2, 2$; $P = 0.424$). Tagging season had a significant effect on RPE ($F = 13.536$; $df = 1, 2$; $P = 0.003$). Direction also significantly affected RPE ($F = 5.329$; $df = 1, 2$; $P = 0.022$). Spring-tagged lake trout showed no directional preference in movement ($t = -1.78$; $df = 13$; $P = 0.098$). However, fall-tagged lake trout moved significantly more often to the south than to the north ($t = -3.41$; $df = 13$; $P = 0.004$).

Density Dependence

The dispersal radius for lake trout tagged in spring was correlated with adult population density in the Clay Banks area, but the same was not true for lake trout tagged in fall. The dispersal radius increased as a function of adult population density for spring-tagged lake trout ($F = 9.17$; $df = 1, 8$; $P = 0.03$) but not for fall-tagged fish ($F = 0.17$; $df = 1, 8$; $P = 0.69$; Figure 5).

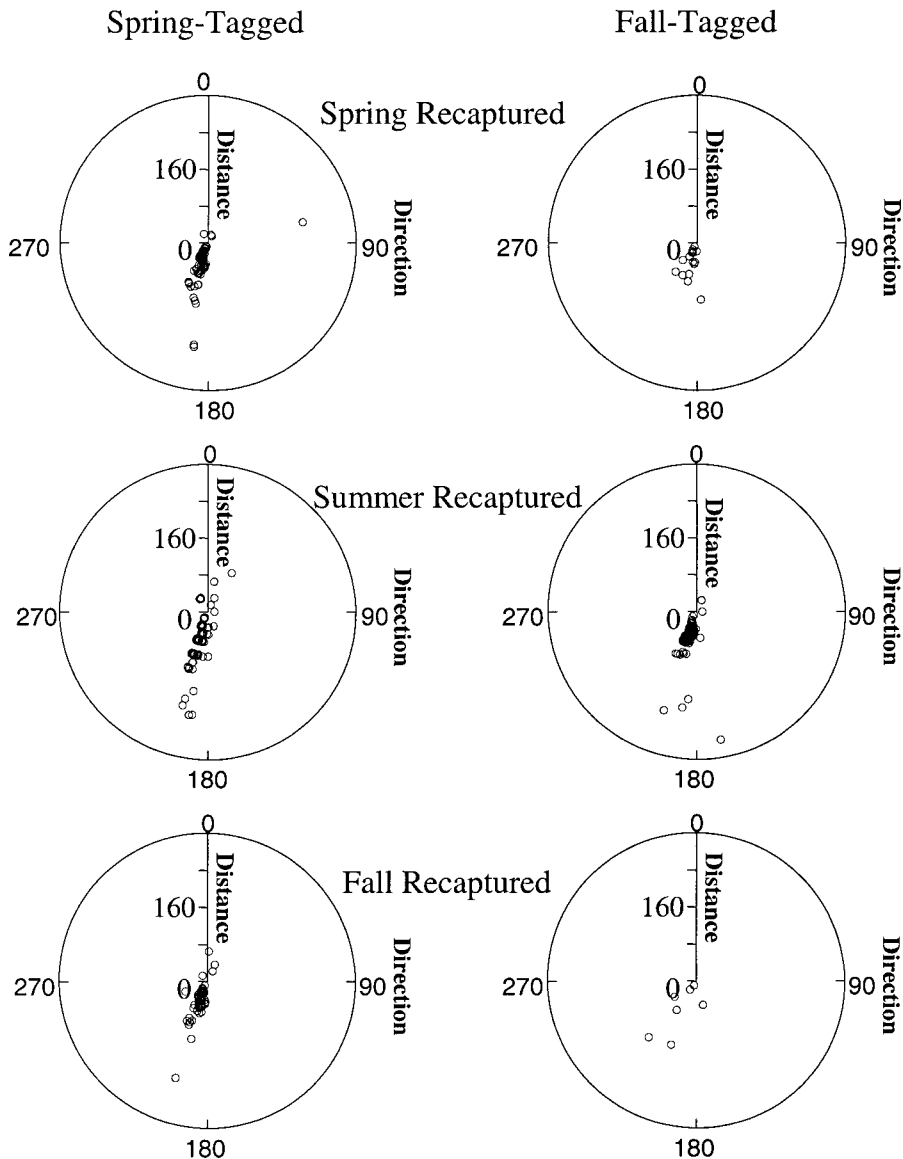


FIGURE 4.—Recoveries of spring- and fall-tagged lake trout within 1 year of tagging in angling fisheries in spring, summer, and fall, 1983–1996. The centers of the large circles represent the tagging location and the small open circles the locations of recaptures as a function of the distance (km) and direction (degrees from true north) from the tagging location.

Discussion

Our results suggest that 90% of the lake trout tagged at Clay Banks remained within 68.4 km of the tagging location regardless of tagging season, recapture season, or population density. Similarly, Smith and Van Oosten (1939) found that 77% of tagged lake trout were caught within 80 km of the tagging location in western Lake Michigan. Rybicki and Keller (1978) found that 72–90% of the

adult lake trout tagged in fall 1973 and 1974 in northeastern Lake Michigan were recaptured within 32.2 km of the tagging location by 1976. Rybicki (1990) found that 88–98% of yearling lake trout in Lake Michigan's Northern Refuge were captured in the immediate vicinity of the reefs where they were stocked that spring. These same fish dispersed as far as 120 km by age 2 and had traveled to southern Lake Michigan by ages 3 and

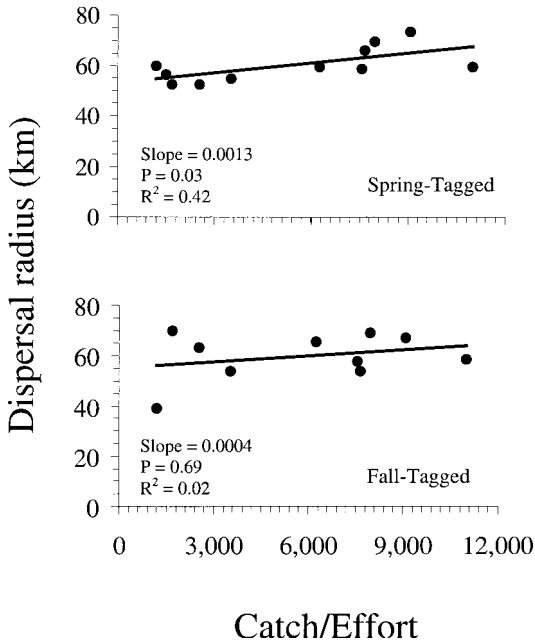


FIGURE 5.—Annual estimates of the dispersal radius of tagged lake trout in relation to adult lake trout population density in the Clay Banks area of northwestern Lake Michigan. Population density was indexed by the spring pound-net catch per effort (number per 50 nights).

4 (Rybicki 1990). Determination of lake trout dispersal radii may have been affected by the true targeted effort of anglers. Anglers targeting lake trout may use different techniques than anglers targeting Pacific salmon *Oncorhynchus* spp. The salmonid-targeted effort used in our calculations did not discriminate among species. However, we are confident that standardizing by salmonid angler effort was superior to no standardization at all.

Fish populations are often divided into discrete stocks that spawn at different locations or seasons (Wheeler and Winters 1984). Fall-tagged lake trout in the Clay Banks area of northwestern Lake Michigan could therefore be defined as the Clay Banks spawning stock. This spawning stock occupied an area within 56–61 km of the spawning area. Spring-tagged lake trout occupied a slightly larger area of 64–69 km. The difference in area occupied was likely due to the mixing of populations during spring and early summer, when spring-tagged fish were tagged. Because fish from other spawning stocks were probably tagged at Clay Banks in spring, when movement was quantified with respect to Clay Banks the result was a slightly larger area of occupation. A higher proportion of immature lake trout may have been included in the

spring sampling as well. Although the length and age distributions were similar for spring- and fall-tagged lake trout (Wisconsin Department of Natural Resources, unpublished data), we do not know the maturity for spring-tagged lake trout. Perhaps immature fish were more likely to move greater distances.

The spatial resolution of the data used in our study may have prevented us from discerning the migratory patterns (defined as seasonal movement differences; Clarke 1954) of lake trout in Lake Michigan. Migration assumes that fish leave an area and then return. Rahrer (1968) found that lake trout tagged during spawning at Gull Island Shoal in Lake Superior were recaptured closer to the shoal in the fall than in other seasons. If the same were true for Lake Michigan, one would expect that the dispersal radius would be smaller in the fall (around the spawning season) than in spring and summer. Our results did not show this pattern. For us to detect such a pattern, mass migrations of lake trout would have had to occur. This pattern may have been further obscured by differences in the months in which effort estimates were made and in lake trout angling season closures. For example, effort for the months of October and November was combined in Wisconsin waters. Lake trout harvest regulations have also changed over the study period. The Clay Banks Refuge, established in 1986 and removed in 1995, prohibited anglers from targeting lake trout within its boundaries. Wisconsin's lake trout angling regulations included a year-round open season with a daily bag limit of three and a minimum length limit of 254 mm in 1984 and 1985. From 1986 to 1994, the season was limited to the period from 1 May to Labor Day (in early September) and the daily bag limit was reduced to two. From 1995 to 1997, the open season was extended to 31 October. Lake trout angling regulations in the rest of Lake Michigan have also changed over the study period. Early season closures (i.e., prior to spawning) may have led to a misrepresentation of fall movement patterns after 1985.

Tagging-site fidelity calculations indicated that the lake trout in northwestern Lake Michigan do indeed return to the same location in successive years during spawning, similar to lake trout in Lake Superior (Buettner 1961; Rahrer 1968; Pycha 1973; Swanson 1973). The literature on lake trout homing, however, is ambiguous. Rybicki and Keller (1978) indicated that lake trout tagged in north-eastern Lake Michigan in 1973 and 1974 showed a strong tendency to home to their tagging site

during the spawning season. MacLean et al. (1981) suggested that lake trout in Lake Opeongo, Ontario, did not home to their natal shoal. Instead, the authors noted that the fish moved between shoals at spawning time. Martin (1960) indicated that the lake trout in an Algonquin Park lake demonstrated homing behavior but that they also spawned on newly created artificial reefs. Wheeler and Winters (1984) found average homing rates (calculated in much the same way as our tagging-site fidelity) of 81% for Atlantic herring. Sockeye salmon *O. nerka*, which demonstrate a high degree of homing, had homing rates over 90% (Harden Jones 1968). The lake trout in northern Lake Michigan returned to the area where they were tagged at a lower proportion than was the case with species that are known to home, but not substantially so. However, lake trout tagged in northern Lake Michigan in the spring were just as likely to be recaptured in the same location in a successive spring as lake trout tagged during spawning in the fall and recaptured in a succeeding fall. Lake trout did indeed return to the same spawning reefs in successive years, but it appeared that these fish generally occupied the same general area throughout the year and did not demonstrate distinct movement patterns. Our results tend to agree with those of Martin and Olver (1980), who stated that lake trout are nomadic and move in response to factors such as spawning, food, and environmental conditions but that some movement is simply random.

Our results show that spring-tagged lake trout did not display a directional preference. This too may be attributed to the mixing of spawning stocks or that of immature fish with adults during spring. However, fall-tagged fish tended to move south more than north, indicating that the Clay Banks spawning stock of lake trout appeared to generally move to the south after spawning. Rybicki and Keller (1978) found that of the lake trout tagged in northeastern Lake Michigan and recaptured more than 16 km from the tagging site, 55% moved southward and 35% northward along the eastern shoreline of the lake. Smith and Van Oosten (1939) noted that lake trout tagged at Port Washington, Wisconsin (along the westcentral shore approximately 130 km south of Clay Banks), tended to move northward. Swanson (1973) noted that lake trout in Lake Superior moved in relation to the prevailing water currents, that is, away from the spawning areas with the prevailing currents and back toward spawning reefs against those currents (Swanson 1973). In the northern basin of Lake Michigan, nearshore currents tend to converge

around the Clay Banks area (Harrington 1895), so that regardless of the direction in which lake trout move away from the tagging area, they will always be against the prevailing surface water currents.

Our results suggest that spring-tagged lake trout expanded the area they occupied as the density of adult lake trout increased. Martin and Olver (1980) indicated that the search for food is an important factor affecting lake trout movements. As population density increased in the Clay Banks area, lake trout may have had to expand their range in search of food. Bjornn (1971) found that population density modified the migration patterns of subyearling and yearling steelhead *O. mykiss* in two Idaho streams. Grant and Kramer (1990) found that emigration increased with population density for juvenile salmonids in streams. Such salmonids often defend feeding territories, which limits population density by encouraging emigration (Grant and Kramer 1990).

Management Implications

Estimates of dispersal distance may be used to determine stocking strategies for lake trout. Stocked lake trout generally remain in the area where they were stocked (Buettner 1961; Pycha et al. 1965; Hesse 1969). The area occupied increases with population density, so stocking more lake trout may cause fish to emigrate from a desired area rather than increasing the local population density. In the context of lake trout rehabilitation in Lake Michigan, which focuses on stocking refuges in an attempt to develop naturally reproducing stocks (Holey et al. 1995), stocking rates should be moderated after adult stocks reach the point where dispersal radius increases.

Our analysis of dispersal radii for lake trout, which are based on RPE as a function of distance (Figure 6), can be used to estimate the effectiveness of refuges created to protect this species in Lake Michigan. These refuges vary in size from the approximately 650-km² former Clay Banks Refuge (1986–1995) to the 1,550-km² Northern Refuge and the 2,859-km² Southern Refuge. For the refuges in existence today, the furthest distance from the center to the border is about 32 km (Holey et al. 1995). Assuming that the center of the lake trout distribution in the refuge coincides with the geometric center of the refuge, each Lake Michigan refuge would protect at best 55–70% of the lake trout population around which the refuge was centered, depending on the season. Therefore, 30–45% of those lake trout may leave the refuges. Such emigration may have the same effect as mor-

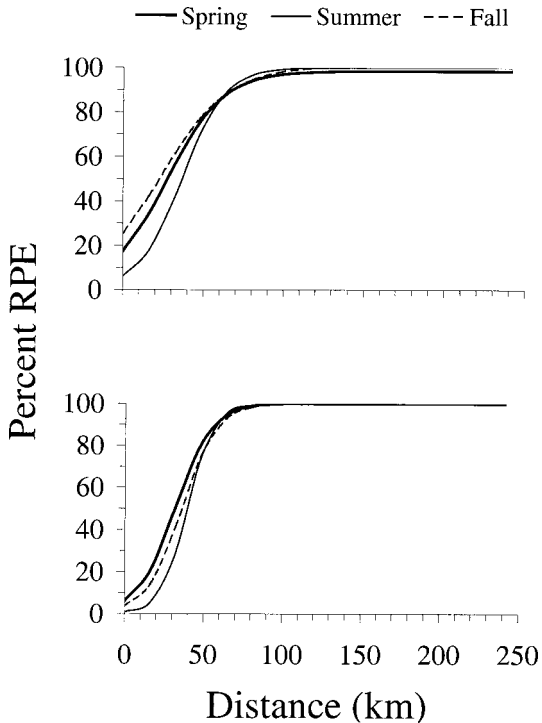


FIGURE 6.—Percent of recaptures per unit effort (RPE) as a function of distance from the tagging location for lake trout tagged in northwestern Lake Michigan during 1983–1996 and recaptured by anglers during 1983–1997. The upper panel is for spring-tagged lake trout and the lower panel for fall-tagged lake trout. The lines depict recapture seasons.

tality if fish move permanently or die before returning. Thus, the lake trout refuges in Lake Michigan may not be large enough to achieve the total annual mortality limit of 40% deemed necessary for lake trout rehabilitation (Holey et al. 1995). Based on our understanding of lake trout movements in northwestern Lake Michigan, protecting 90% of an adult stock would require a refuge centered on a spawning area that was at least 68 km from the center to its border, a minimum of 18,496 km² (for a square refuge).

Lake trout movement tended to be greater along the western shoreline of northern Lake Michigan than across open-water areas of the lake. Even though most of the effort exerted to recapture lake trout in this study was near shore rather than in the middle of the lake (Eggold, personal communication), there appeared to be very little movement directly across the lake. Although the lake trout in our study would only have had to travel about 80 km directly east to reach the Michigan

shore, only 9 recaptures were made directly across the lake, compared with 182 along the western shore at distances of more than 80 km. Our results suggest that areas of open water might separate lake trout stocks in northern Lake Michigan and that fish tagged while spawning at Clay Banks tend to move more to the south.

As our results indicate that lake trout occupied an area with a radius of approximately 68 km, lake trout populations should be managed accordingly. For management areas adjacent to jurisdictional boundaries, such as the Wisconsin–Illinois, Indiana–Michigan, and Wisconsin–Michigan borders, lake trout should be managed as shared stocks. Fishery regulations in those areas, such as season length, bag limits, and size limits, should recognize that lake trout occupying these areas move freely back and forth across state boundaries. If a strict regulation is based solely on geographic location, it may not protect the targeted population. Instead, regulations should be set to protect populations that are centered on known spawning locations. For example, the location subject to a larger minimum length limit could be determined by the distance from the known spawning location of the population of interest.

Lake trout movements should also be considered when modeling contaminant dynamics in Lake Michigan. Lake trout are an important vector of contaminant transport because they are long-lived (Madenjian et al. 1993). Our results suggest that lake trout remain within a relatively discrete area regardless of season. Our data also show that efforts to model lake trout contaminant transport in Lake Michigan may not have to consider fish more than 68.4 km from the location of the stock being sampled to capture 90% of that population.

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