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[Article]

Relative Abundance, Site Fidelity, and Survival of Adult Lake Trout in Lake Michigan from 1999 to 2001: Implications for Future Restoration Strategies

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Abstract.—We compared the relative abundance of lake trout *Salvelinus namaycush* spawners in gill nets during fall 1999–2001 in Lake Michigan at 19 stocked spawning sites with that at 25 unstocked sites to evaluate how effective site-specific stocking was in recolonizing historically important spawning reefs. The abundance of adult fish was higher at stocked onshore and offshore sites than at unstocked sites. This suggests that site-specific stocking is more effective at establishing spawning aggregations than relying on the ability of hatchery-reared lake trout to find spawning reefs, especially those offshore. Spawner densities were generally too low and too young at most sites to expect significant natural reproduction. However, densities were sufficiently high at some sites for reproduction to occur and therefore the lack of recruitment was attributable

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to other factors. Less than 3% of all spawners could have been wild fish, which indicates that little natural reproduction occurred in past years. Wounding by sea lamprey *Petromyzon marinus* was generally lower for Seneca Lake strain fish and highest for strains from Lake Superior. Fish captured at offshore sites in southern Lake Michigan had the lowest probability of wounding, while fish at onshore sites in northern Lake Michigan had the highest probability. The relative survival of the Seneca Lake strain was higher than that of the Lewis Lake or the Marquette strains for the older year-classes examined. Survival differences among strains were less evident for younger year-classes. Recaptures of coded-wire-tagged fish of five strains indicated that most fish returned to their stocking site or to a nearby site and that dispersal from stocking sites during spawning was about 100 km. Restoration strategies should rely on site-specific stocking of lake trout strains with good survival at selected historically important offshore spawning sites to increase egg deposition and the probability of natural reproduction in Lake Michigan.

The last native lake trout *Salvelinus namaycush* were observed in Lake Michigan in 1954 shortly before they were extirpated from overfishing and predation by sea lamprey *Petromyzon marinus* (Eschmeyer 1957; Holey et al. 1995; Hansen 1999). After effective sea lamprey control began in 1965, hatchery-reared lake trout (mostly yearlings at 13–15-months-old and some fall fingerlings at 10–11 months) were stocked annually to restore populations. During the last 40 years, an average of 2.7 million lake trout of various strains have been stocked annually (Figure 1a). From 1965 to the early 1980s, most fish were released at shoreline sites that were accessible to stocking trucks, with little thought given to the suitability of the nearby habitat for spawning. It was assumed that these stocked fish would, at maturity, locate suitable spawning habitat

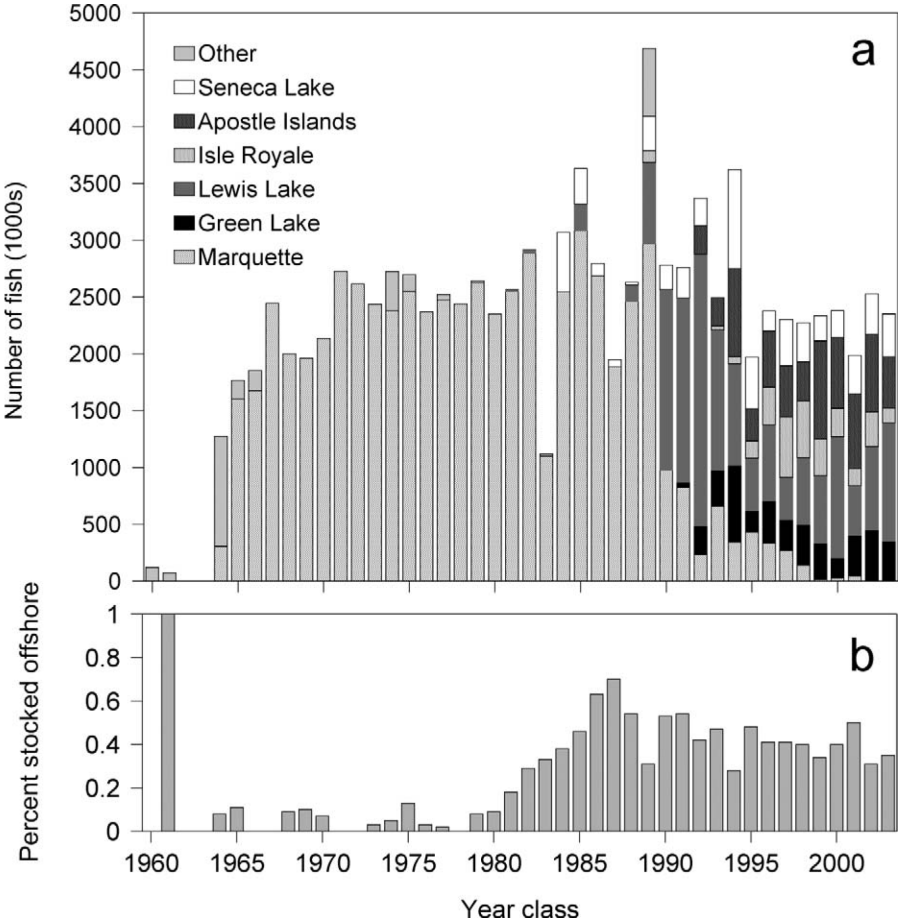

FIGURE 1.—**(a)** Numbers of lake trout stocked into Lake Michigan by year-class and strain during 1959–2001 and **(b)** percent stocked at offshore locations, 1960–2001.

and reproduce. Unfortunately, many fish simply returned to the sites where they were stocked to spawn regardless of habitat suitability. Although some natural reproduction has been documented in Lake Michigan (Dorr et al. 1981; Jude et al. 1981; Wagner 1981; Rybicki 1991; Marsden 1994; Jonas et al. 2005), sustained recruitment of wild fish has not occurred (Holey et al. 1995; Madenjian and DeSorcie 1999).

Many factors have been suggested for the lack of sustained natural reproduction by lake trout in Lake Michigan (Eshenroder et al. 1999; Bronte et al. 2003). Failure was partially attributed to the apparent inability of hatchery-reared fish to locate and spawn at suitable sites, which has been problematic elsewhere in the Great Lakes (Eshenroder et al. 1984; Krueger et al. 1986). To expedite colonization, stocking strategies in Lake Michigan were modified in 1985 to include transporting lake trout by boat to historically important offshore spawning reefs for release (LMLTTC 1985; Holey et al. 1995); since then, about 50% of the fish have been placed at such locations (Figure 1b). Two offshore refuges, the Northern Refuge and the Southern Refuge (which includes the Mid-Lake Reef complex in south-central Lake Michigan) were also created to protect fish from commercial and recreational exploitation (Figure 2). Stocking rates prescribed for these refuges were greater than for other areas to expedite the establishment of large parental stocks at these historically important locations. Hatchery-reared lake trout have survived well enough to contribute to fisheries, but few areas (e.g., Clay Banks, East Reef, and Sheboygan Reef) have developed significant spawning stocks composed of older fish (12+ years; Holey et al. 1995). Less-abundant spawning stocks composed of younger fish have become established in northern Lake Michigan (Madenjian and DeSorcie 1999).

The efficacy of stocking lake trout directly at specific sites to develop spawning aggregations has not been evaluated in Lake Michigan; hence a comparison of stocked and unstocked sites was warranted. Our primary objective was to determine how effective site-specific stocking is for recolonizing historically important spawning reefs and to document the ability of lake trout to colonize unstocked spawning sites that were also historically important in Lake Michigan. We compared the relative abundance of lake trout spawners aggregating in fall on stocked sites to those that were unstocked for both onshore and offshore sites. Our null hypothesis was that the relative abundance of spawners at stocked sites should not be different from the abundance at unstocked sites, and the alternate hypothesis was that stocked sites will have higher densities of spawners than unstocked sites. Understanding how well hatchery-reared lake trout colonize reefs will improve management strategies that maximize the potential for reproductive success and hopefully foster sustained recruitment. We also compared the relative abundance of spawners against previously established benchmarks for lake trout parental stocks under restoration to further measure adequacy.

Data from this primary objective resulted in other measures to evaluate the overall potential for significant natural reproduction by parental stock regardless of stocking history. There were five secondary objectives. First, to examine the age, size, and sex composition of the spawner aggregations among sites and regions of the lake to further evaluate the adequacy of the parental stock. Second, to determine the extent of past natural reproduction based on the presence of unclipped adults (all hatchery-reared fish are finclipped). Third, to compare the relative survival of strains stocked as yearlings with coded wire tags recaptured during spawning and to build upon previous survival comparisons (McKee et al. 2004). (Those strains that demonstrate superior survival would be recommended as possible candidates for increased hatchery production for future stocking. Our null hypothesis was that survival would not differ across strains.) Fourth, to compare sea lamprey wounding across strains and regions of the lake to evaluate the effects of their predation on lake trout survival. Fifth, to estimate the dispersal and site fidelity of various lake trout strains stocked at eight sites (Figure 2). We present a lakewide evaluation of spawning stocks in Lake Michigan and discuss the implications of our findings for the restoration program.

Stocking History

The U.S. Fish and Wildlife Service has stocked most of the lake trout for restoration in Lake Michigan (Holey et al. 1995). Eight strains have been introduced since 1985 (Figure 1a). Strains were chosen from available donor populations established from introductions of extant Lake Michigan stocks (Green Lake, Lewis Lake, and Jenny Lake; Krueger et al. 1983; Krueger and Ihssen 1995), from remnant wild populations from Lake Superior (Marquette, Apostle Islands, and Isle Royale), and from the Finger Lakes region of New York (Seneca Lake, Lake Ontario; Marsden et al. 1993). The Green Lake, Seneca Lake, and Lake Ontario strains were selected because their donor stocks showed traits of spawning on deepwater reefs that were historically important sources of recruitment in Lake Michigan (Dawson et al. 1997). The Jenny Lake fish were introduced because they were thought at that time to be genetically similar to siscowet lake trout from Lake Superior (Krueger et al.

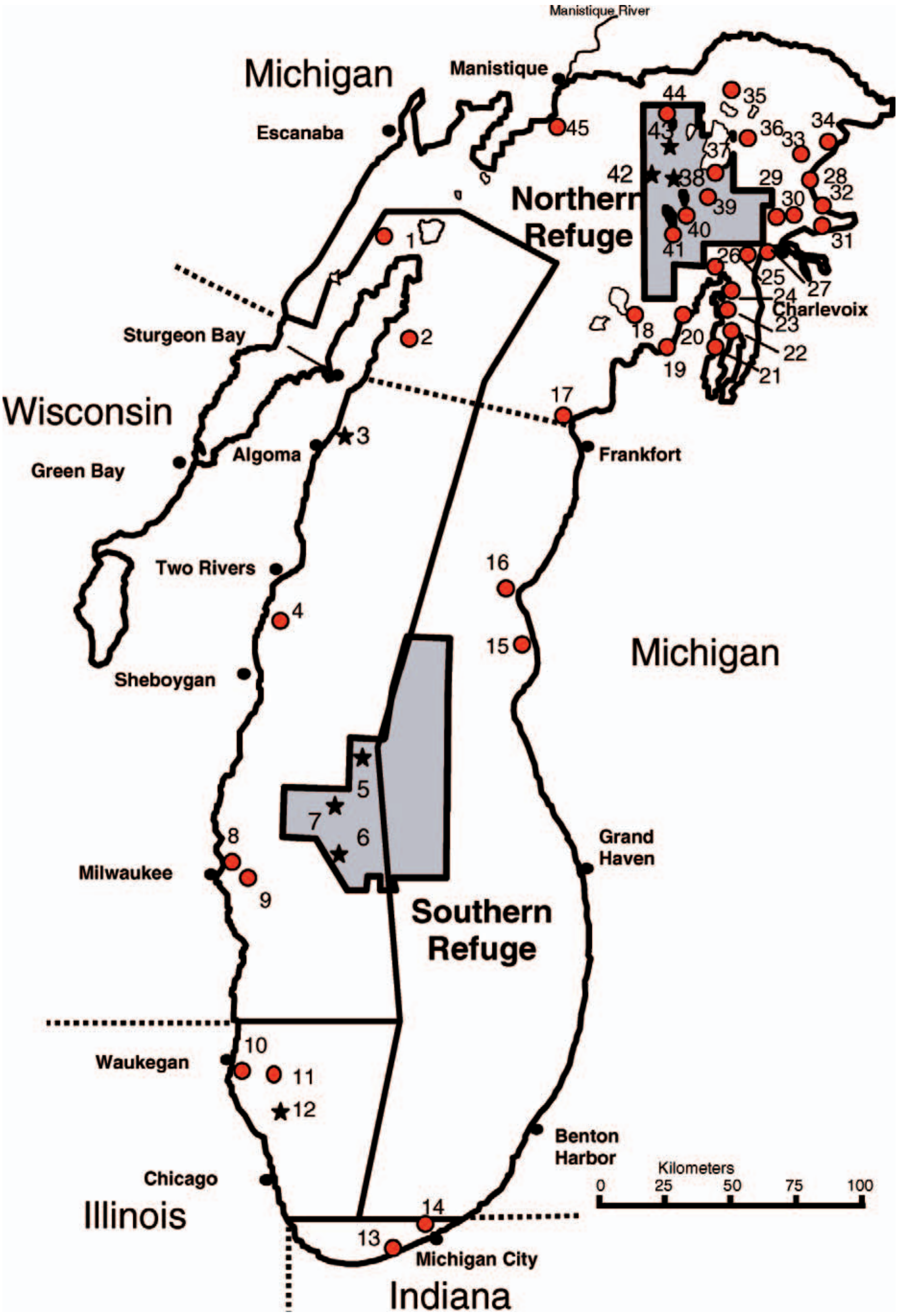

FIGURE 2.—Map of Lake Michigan showing the locations of refuges and the sites sampled for lake trout spawners during 1999–2001. Sites marked with stars were stocked with coded-wire-tagged yearling lake trout. Site names and numbers are found in Tables 1 and 3. Site 7 is the Northeast Reef, which was stocked with coded-wire-tagged fish but not sampled for lake trout spawners. The dashed line separates the northern and southern regions used for comparisons of age, size, and sea lamprey wounding.

1989) and more likely to colonize offshore areas. The remaining strains are known to prefer shallow-water habitats for feeding and spawning.

The evaluation of strain survival and dispersal was centered in the two refuges and at Clay Banks near Sturgeon Bay, Wisconsin, and Julian's Reef near Waukegan, Illinois. All fish stocked at Boulder Reef, Gull Island Reef, and Richard's Reef in the Northern

TABLE 1.—Classification of spawning sites (stocked, unstocked, onshore, and offshore) sampled in Lake Michigan during fall 1999, 2000, and 2001. The numbers in parentheses refer to the sampling sites indicated in Figure 2.

Stocked–onshore ($N = 11$)	Stocked–offshore ($N = 8$)	Unstocked–onshore ($N = 13$)	Unstocked–offshore ($N = 12$)
Bay Harbor (31)	Boulder Reef (42)	Big Stone Bay (27)	Big Reef (29)
Clay Banks (3)	East Reef (6)	Cathead Bay (26)	Dahlia Shoal (33)
Green Can Reef (9)	Gull Island Reef (43)	Fisherman's Island (25)	Fox Island, north (40)
Good Harbor Reef (19)	Julian's Reef (12)	Good Hart Reef (34)	Fox Island, south (41)
Lee Point (21)	Michiana Reef (14)	Ingall's Point (24)	Head of Beaver (37)
Ludington Reef (15)	Richards Reef (38)	Lansing Shoal (35)	Hog Island Reef (36)
Northeim Reef (4)	Sheboygan Reef (5)	Menonaqua (32)	Irishman's Grounds (30)
Old Mission Point (22)	Trout Island Shoal (44)	North Reef (20)	Jacksonport Reef (2)
Point Betsie Reef (17)		Northport/Cherry Home (23)	North Manitou Shoal (18)
Portage Point Reef (16)		Pt. Aux Barques (45)	Middle Ground (39)
South Milwaukee Reef (8)		Port of Indiana (13)	Waukegan Reef (11)
		Seven Mile Point Reef (28)	Whaleback Shoal (1)
		Waukegan Shore (10)	

Refuge; at East Reef, Sheboygan Reef, and Northeast Reef in the Southern Refuge; and at Clay Banks and Julian's Reef received a coded wire tag in the snout and an adipose fin clip to identify strain, year-class, and the site stocked. Mostly Lewis Lake strain fish were stocked at Clay Banks, and mostly Green Lake strain fish were stocked at Julian's Reef. The tagged strains stocked into the Northern Refuge were mostly Lewis Lake, Apostle Islands, Marquette, and Isle Royale, while Seneca Lake, Green Lake, and Marquette strains were mostly stocked in the Southern Refuge. The Marquette strain did not receive coded wire tags after the 1993 year-class and was removed from the strain comparison even though this strain was stocked thereafter. These fish were "replaced" by the Isle Royale strain in the evaluation. For 20 years prior to 1985, Marquette was the predominant strain stocked into Lake Michigan and contributed to the buildup of populations there (Holey et al. 1995) and in other Great Lakes (Elrod et al. 1995; Eshenroder et al. 1995b; Hansen et al. 1995). For this study, data for the Jenny Lake and Lewis Lake strains were combined (hereafter Lewis Lake) because they are genetically similar (Krueger et al. 1983). We also combined data of the Lake Ontario and Seneca strains (hereafter, Seneca Lake) because they were also genetically similar (Marsden et al. 1993).

Methods

Survey methods.—We measured the relative abundance of lake trout spawners at 44 sites in Lake Michigan from mid-October to early November during 1999–2001 (Table 1). Reefs were selected based on putative historical importance (Dawson et al. 1997) and on recent stocking history to provide contrast in stocking numbers and proximity to shore. Spawning populations were sampled with overnight sets of 244-m gangs of gill nets made of two 30.5-m panels each of 114-, 127-, 140-, and 152-mm stretch-mesh sizes. Gill-net mesh was constructed of 210/3 or 104 (152-mm mesh only) multifilament nylon twine, 1.8 m high, and hung on the half-basis. At least three lifts were made on each reef in each year over a 2-week period during spawning for at least 2 years during the 3-year period. Every effort was made to sample when spawning was at or near peak based on previous experience at those sites. Total length (mm), sex, maturity, reproductive stage, and fin clips (or lack thereof) were recorded for each lake trout captured, and scale samples collected for year-class determination. Sea lamprey wounds were classified (King 1980) and summarized by standard length-groups for the Great Lakes (Pycha and King 1975). Fish with adipose fin clips, which identified them as having coded wire tags, where sacrificed for tag removal to determine strain, year-class, and stocking site. Year-class membership was determined from coded-wire tags or a combination of the number of annuli on scales and fin clip history.

Data analysis.—We expressed the relative abundance of lake trout at each reef as the mean of catch per unit effort (CPUE) defined as the number of fish per kilometer of gill net per night across all lifts in all years. Lake trout spawning reefs were grouped into four categories based on stocking history (stocked versus unstocked) and proximity to the shoreline (onshore versus offshore) to determine the effect of location and stocking history on the development of spawning aggregations (Table 1). The age at 50% maturity for lake trout in Lake Michigan ranges from 4.3 to 6.3 years for males and 5.5–7.4 years for females (Madenjian et al. 1998), and the maximum age of lake trout in Lake Michigan rarely exceed 15 years. Based on this maturity schedule, reefs were only considered "stocked" if they received fish from the 1979–1994 year-classes. Spawning sites were classified as onshore if they were less than 8 km from the shoreline and followed previous classifications (onshore, offshore) by Dawson et al. (1997). To test for differences ($P \leq 0.05$) in relative abundance among the four site categories, we treated each lift within each category, regardless of site, as an observation and compared the $\log_e$ transformed CPUEs using analysis of variance (ANOVA) and Bonferroni post hoc tests.

To determine whether the parental stock was reasonably sufficient, the mean CPUE of spawners at each site was compared with a mean CPUE of 164 fish/km of net lifted, which is the average abundance associated with natural reproduction by hatchery-reared adults in the Great Lakes (Selgeby et al. 1995). Natural reproduction by hatchery-reared lake trout was observed at spawner CPUEs of 55–444 fish/km of net at Lake Superior sites and temporarily in Lake Michigan. Peck (1979) previously classified spawning populations of hatchery-reared lake trout in Lakes Michigan, Huron, and Superior as "poor" when CPUE was less than 33 fish/km of net lifted, "fair" between 33 and 163 fish/km, and "good" greater than 164 fish/km, based on comparisons with wild spawning populations in Lake Superior. Both classifications expect some reproduction to occur at CPUEs greater than 33 fish/km of net lifted. Our reference metric of 164 fish/km represents a density of spawners that should produce recruits. Reproduction should also be possible at lower densities as observed in wild populations in Lake Superior (Peck 1979; Swanson and Swedburg 1980; Schram et al. 1995), where fewer recruitment bottlenecks (i.e., predation on eggs and fry) are present. This assumes that hatchery-reared adults have a similar reproductive efficiency as wild adults, which has been suggested for populations in Lake Superior (Richards et al. 2004).

To determine the adequacy of the age structure of the parental stock, the mean ages of spawners at each site were calculated across years and the values directly compared with a maturity schedule for Lake Michigan. Full cohort maturity in Lake Michigan was reported at about age 7 for males and females (Madenjian et al. 1998). Mean ages at or below age 7 may suggest an age structure too young for significant egg deposition for a long-lived species like lake trout.

Natural reproduction in past years was evaluated by determining the proportion of fish without fin clips captured in the adult stock. All hatchery-reared fish are marked prior to stocking with a year-class-specific fin clip that is repeated every 5 years, or a coded wire tag with an adipose clip. Since 1990, annual fin clip efficiency in U.S. Fish and Wildlife Service hatcheries has averaged 94% (or 6% without fin clips); hence, unclipped lake trout at levels greater than 6% (given adequate sample sizes) is probably suggestive of natural reproduction.

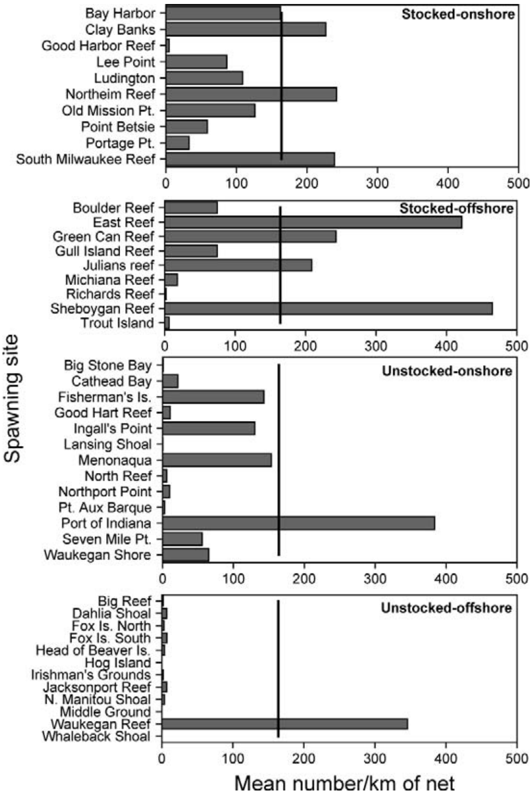

FIGURE 3.—Mean relative abundance of spawning lake trout at 44 locations in Lake Michigan during October and November 1999, 2000, and 2001. The solid vertical line represents the average density at which natural reproduction has been observed in the Great Lakes (Selgeby et al. 1995).

The relative survival of lake trout strains was estimated by comparing the average CPUE in all lifts (including zero observations) for each strain and year-class combination in all capture years corrected for the numbers stocked. Comparisons were restricted to the 1995–1997 year-classes of Green Lake, Lewis Lake, Apostle Islands, Isle Royale, and Seneca Lake, and the 1985, 1989–1992 year-classes of Lewis Lake, Seneca Lake, and Marquette as these year-classes were all tagged and represented in the catches. Data were $\log_e$ transformed, significant differences ($P \leq 0.05$) were detected using ANOVA, and survival differences among strains were identified with Bonferroni post hoc tests.

To investigate differences in sea lamprey wounding among lake trout strains or among regions of Lake Michigan, logistic regression was used (Schneider et al.

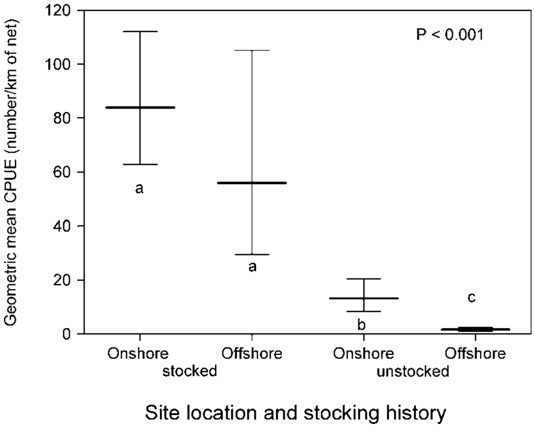

FIGURE 4.—Mean relative abundances of lake trout spawners captured at stocked and unstocked onshore and offshore reefs in Lake Michigan. Whiskers represent 95% confidence intervals; means with the same letter are not significantly different.

1996; Madenjian et al. 2004) to relate strain and lake region to the probability of a lake trout's bearing an A1, A2, or A3 sea lamprey wound (King 1980). First, we determined whether sea lamprey attack rates varied significantly among the Marquette, Seneca Lake, Lewis Lake, Green Lake, and Apostle Islands strains. For this analysis, data were pooled for all year-classes and all sites, and the Marquette strain was chosen as the reference strain. Second, we determined whether sea lamprey attack rate was significantly higher in the northern Lake Michigan (north of a line from Sturgeon Bay to Point Betsie) compared with southern Lake Michigan; the reference for this analysis was southern Lake Michigan. Thirdly, we determined whether the sea lamprey attack rate was significantly higher in the onshore waters of the lake compared with the offshore waters of the lake; the offshore region was the reference region for this analysis. Lastly, we determined whether the sea lamprey attack rate varied significantly among the onshore-north, offshore-north, onshore-south, and offshore-south regions; the offshore-south region was the reference region. The dependent variable in each of these logistic regression analyses was the probability of bearing an A1–A3 mark (as in King 1980). Independent variables in the model included the dummy variables to accommodate strain or region effects and total length of the lake trout. A Wald chi-square statistic was used to assess the significance ($P \leq 0.05$) of strain or region effects.

Stocking site fidelity was determined by calculating the percentage of coded-wire-tagged fish recaptured at each site sampled corrected for effort. The dispersal radius ($X_{0.90}$), from the stocking site was also calculated. This was defined as the straight-line distance from the stocking site within which 90% of the fish were recaptured (similar to Schmalz et al. 2002). First, the cumulative proportion (Y) of recaptures was modeled as a function of the distance from the stocking site, that is,

$$Y = 1/(1 + \beta e^{Kx}),$$

where β is a scaling parameter, and Kx is the rate at which the cumulative proportion of recaptures increases with distance X from the stocking site; then $X_{0.90}$ was estimated using

$$X_{0.90} = (-2.2 - \log_e \beta)/K.$$

Separate models were fit for each stocking site using all strains combined and for each strain for all sites combined. Confidence intervals (95%) for dispersal radii were estimated using the values of the upper and lower Wald confidence intervals for β and K estimated for each site or strain and solving for $X_{0.90.}$

Results

Relative Abundance of Spawners

We captured 7,678 spawning lake trout from 314 gill-net lifts at 44 sites in Lake Michigan during 1999–2001. The relative abundance averaged 95.3 fish/km of net, and ranged from 0.0 at Hog Island Shoal, Middle Ground, and Whaleback Shoal to 465.1 fish/km of net at Sheboygan Reef (Figure 3). Only 10 of the 44 sites had CPUEs at or above our target of 164 fish/km of net (Figure 3). Twenty-six sites exceeded the minimum threshold of 56 fish/km of net from Selgeby et al. (1995). Twenty-one sites had CPUEs greater than 33 fish/km and would be classified as "fair to good" according to Peck (1979). The average CPUE of spawners was higher ($t = -8.1$; df = 312; $P < 0.0001$) at sites in southern (241 fish/km of net) Lake Michigan when compared with northern (46 fish/km of net) sites. The relative abundance of adult lake trout was higher ($F = 61.1$; df = 3, 310; $P < 0.0001$) at stocked sites (both onshore and offshore) compared with unstocked sites (Figure 4). Furthermore, unstocked, onshore sites had higher densities than offshore, unstocked sites.

Age, Size, and Sex Composition

The mean ages of fish captured at most sites ranged from 5.0 to 10.5 years. Twenty-six sites where fish were captured had mean ages of less than 7 years (Figure 5), the age at full cohort maturity. Stocked offshore sites had slightly older fish (9.3 ± 2.6 years [mean ± SD]) than stocked onshore sites (8.3 ± 3.1) and unstocked (7.3 ± 2.6) onshore and offshore sites (6.1 ± 2.5; $F = 151.0$, df = 3, 6,318, $P < 0.0001$). Fish from northern sites (6.4 ± 2.1) were younger than fish

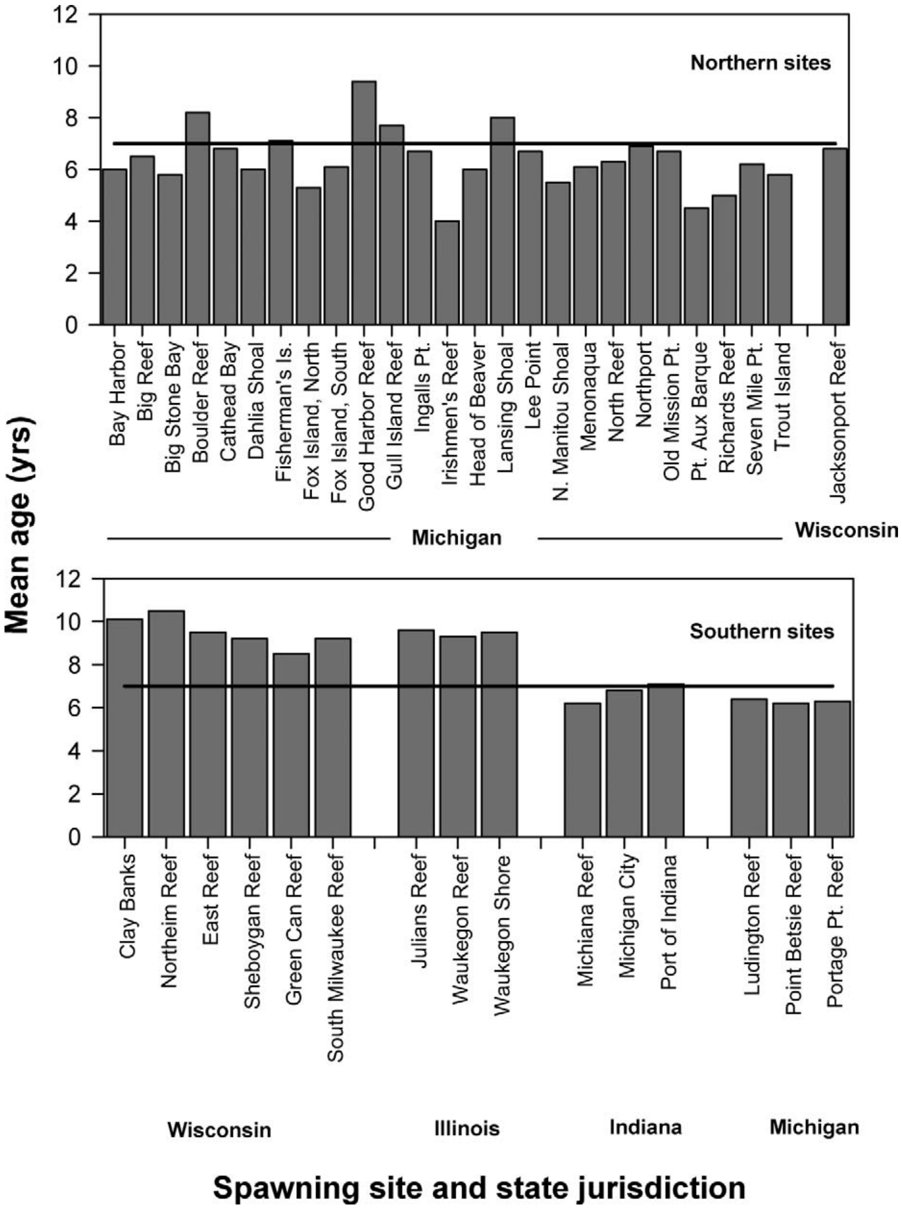

FIGURE 5.—Mean age (years) of lake trout spawners at various sites by state jurisdiction in northern and southern Lake Michigan. The horizontal lines represent the age at full cohort maturity.

from southern sites (9.2 ± 3.0; $t = -29.8$, df = 6, 286, $P < 0.0001$). Smaller fish were also captured at northern sites (666 ± 73 mm) compared with southern sites (725 ± 123; $t = -15.2$, df = 6, 286, $P < 0.0001$). Unstocked offshore sites had the smallest fish (634 ± 79; $F = 20.5$, df = 3, 7,034, $P < 0.0001$) compared with stocked nearshore (709 ± 87) and offshore sites (691 ± 87), and stocked offshore sites (695 ± 158). Females made up between 0% and 100% of the spawners captured at different sites and were 25% of the entire catch across all sites (Figure 6). Low and high percentages of females generally were from sites with low catches.

Natural Reproduction

There was no evidence of past natural reproduction, as indicated by the percentage of unclipped lake trout recovered. Only 2.6% of spawners were observed

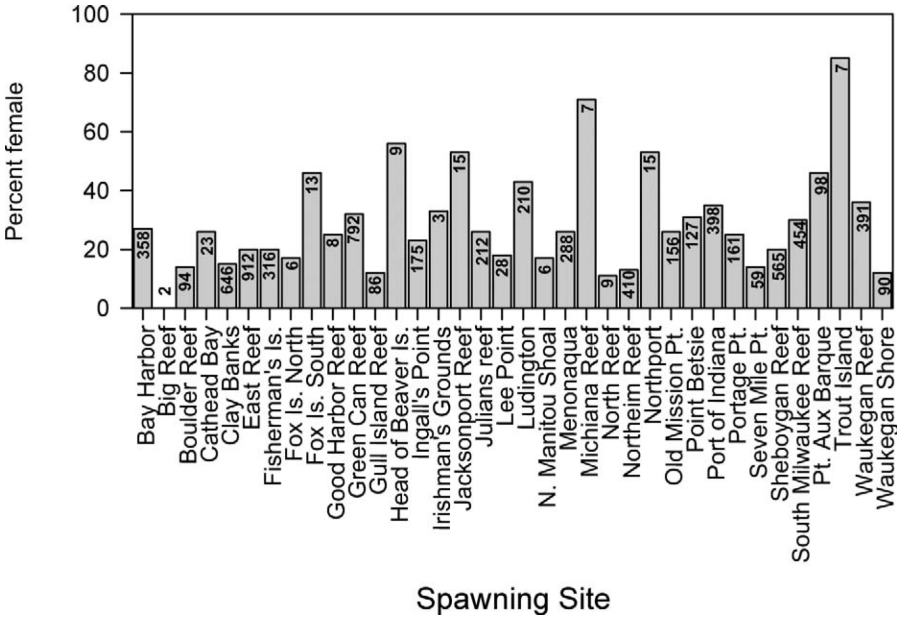

FIGURE 6.—Percentages of female lake trout captured at various spawning sites in Lake Michigan, 1999–2001. The values within the bars are the numbers of fish examined.

without fin clips, and this ranged from 0% at 12 sites to 22% at the head of Beaver Island where only nine lake trout were captured (Figure 7). Year-class-specific percentages of unclipped fish ranged from 0% for most of the year-classes in the 1980s to 7.6% for the 1998 year-classes (data not shown), although most were below the long-term average of 6% and suggest little or no natural reproduction for the 1982–1997 year-classes that composed most of the catch.

Relative Survival among Strains

Relative survival differed among lake trout strains. We recovered 352 Marquette, 497 Lewis Lake, and 458 Seneca Lake coded-wire-tagged fish of the 1985, 1989–1992 year-classes. Relative survival of Seneca Lake fish was almost three times greater than for Marquette or Lewis Lake strains ($F = 20.3$, df $= 2$, 121,905, $P < 0.0001$; Figure 8a). We recaptured 22 Green Lake, 42 Lewis Lake, 9 Isle Royale, 25 Apostle Islands, and 39 Seneca Lake fish from the 1995–1997 year-classes. For these year-classes, differences in survival were apparent ($F = 4.7$, df $= 4$, 121,905, $P = 0.0009$; Figure 8b) but were less definitive. Relative survival of Seneca Lake fish was the highest for these five strains and similar to Lewis Lake and Apostle Islands strains, and was higher than Green Lake and Isle Royale strains. Survival was similar among Green Lake, Lewis Lake, and Apostle Islands strains.

TABLE 2.—Results from the logistic regression analysis of sea lamprey wounding data for lake trout from Lake Michigan 1999–2001. The dependent variable in all regression analyses was the probability of a lake trout bearing an A1–A3 wound (see text); CI = confidence interval.

Data source	Reference strain or lake region	Strain or lake region	Odds ratio (95% CI)	Wald χ^2	P-value
All year-classes and sites pooled	Marquette	Seneca Lake	0.67 (0.41–1.08)	2.85	0.0911
		Lewis Lake	1.22 (0.79–1.91)	0.83	0.3631
		Green Lake	0.79 (0.44–1.44)	0.61	0.4363
		Apostle Islands	2.62 (1.38–5.00)	8.98	0.0027
All strains and year-classes pooled	Southern	Northern	3.40 (2.43–4.76)	53.15	<0.0001
All strains and year-classes pooled	Offshore	Onshore	2.95 (2.11–4.12)	41.77	<0.0001
All strains and year-classes pooled	Offshore–southern	Onshore–northern	4.37 (2.99–6.39)	59.99	<0.0001
		Offshore–northern	2.33 (1.33–4.08)	9.18	0.0024
		Onshore–southern	1.67 (0.91–3.07)	2.84	0.0918

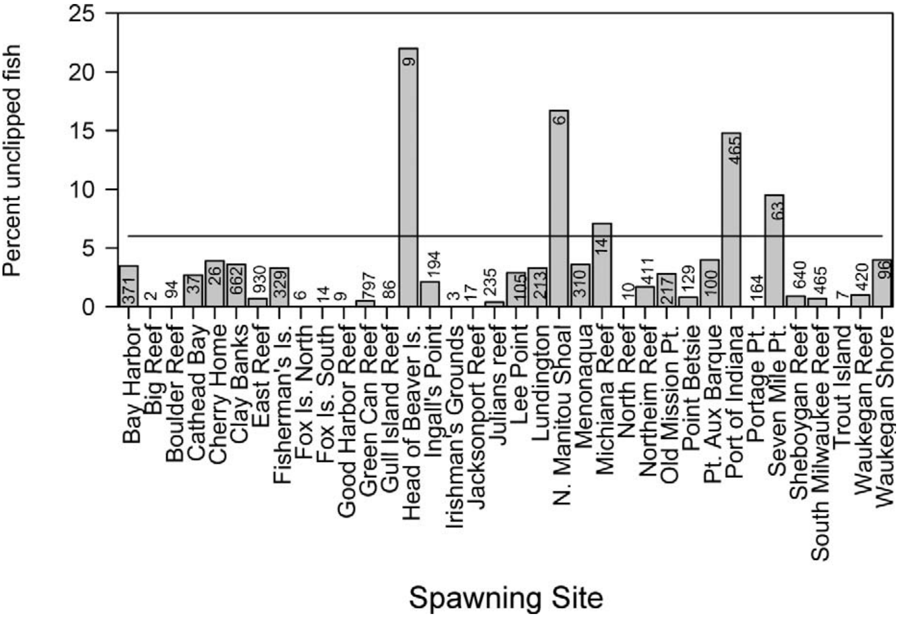

FIGURE 7.—Percentages of unclipped lake trout captured at various spawning sites in Lake Michigan, 1999–2001, compared with the average background rate of unclipped lake trout stocked by federal hatcheries (horizontal line). The values within the bars are the numbers of fish examined.

Sea Lamprey Wounding

Sea lamprey wounding differed among strains and regions of the lake. Wounding (A1–A3 wounds per 100 fish) generally increased with size of lake trout (Figure 9). The Green Lake (5.4) and Seneca Lake (6.8) strains had the lowest wounding rates, followed by Isle Royale (10.0), Lewis Lake (10.1), Marquette (11.8), and Apostle Islands (20.2). Logistic regression analysis on pooled year-classes lakewide (Isle Royale fish were excluded because of low sample sizes) revealed that the Apostle Islands strain was 2.6 times more likely to be attacked by a sea lamprey than the Marquette strain, whereas the Seneca Lake strain was 0.67 times as likely to be attacked compared with the Marquette strain (Table 2). Sea lamprey attack rate was higher for the Apostle Islands strain compared with the Marquette strain (Wald $\chi^2 = 8.98$, df $= 1$, $P < 0.01$), but we detected no other significant differences among strains. Lake trout from sites in northern Lake Michigan were nearly 3.5 times more likely to be attacked than those from southern sites (Wald $\chi^2 = 53.15$, df $= 1$, $P < 0.0001$). Lake trout from onshore sites were nearly three times more likely to be attacked by a sea lamprey that those from offshore sites (Wald $\chi^2 = 41.77$, df $= 1$, $P < 0.0001$). Sea lamprey attack rate was highest for fish from onshore-northern sites and lowest for fish from offshore-southern sites. Lake trout from onshore-northern sites were about 4.4 times (Wald $\chi^2 = 59.99$, df $= 1$, $P < 0.0001$) and fish from offshore-northern sites were 2.3 times more likely to be attacked by a sea lamprey than lake trout from offshore-southern sites (Wald $\chi^2 = 9.18$, df $= 1$, $P < 0.01$). No significant difference was detected between the onshore-southern and offshore-southern waters.

Dispersal and Fidelity to Stocking Sites

Forty percent (20–75% across all sites) of 2,237 spawners with coded wire tags were recaptured at the sites where they were stocked, and many of the remaining fish were captured at sites adjacent to those where they were stocked (Table 3). These adjacent sites were generally stocked as well. Fish stocked in the Northern Refuge dispersed more than fish stocked in the Southern Refuge or at the one onshore stocked site, Clay Banks. None of the fish stocked at Richards Reef were recovered there; these fish were recaptured at 28 other sites, primarily in northern Lake Michigan (Table 3). Most fish stocked at Gull Island and Boulder Reef returned to their stocking site or to nearby sites within or near the refuge. Lake trout stocked in the Southern Refuge were more likely to return there to spawn. More than 70% of the lake trout stocked on the East, Northeast, and Sheboygan Reefs were recaptured at one or more of these three sites. At Clay Banks, the

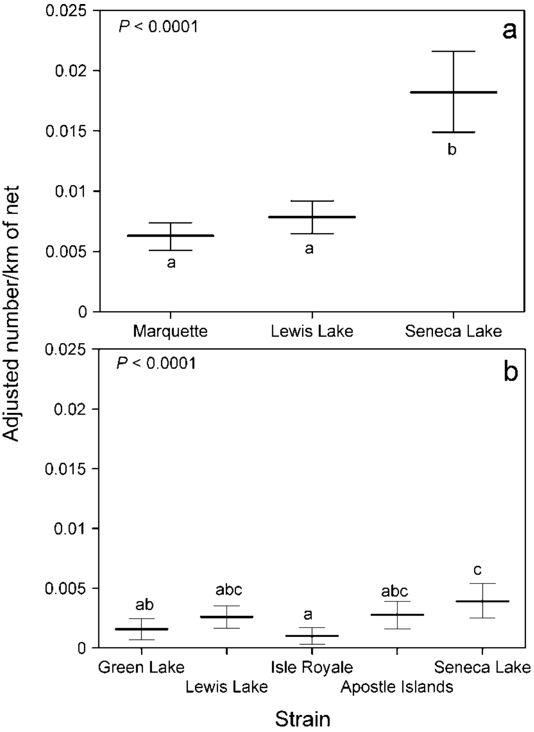

FIGURE 8.—Comparison of the relative survival of lake trout strains of (**a**) the 1985, 1989, and 1990–1992 year-classes and (**b**) the 1995–1997 year-classes in Lake Michigan. Whiskers represent 95% confidence intervals; means with the same letter are not significantly different.

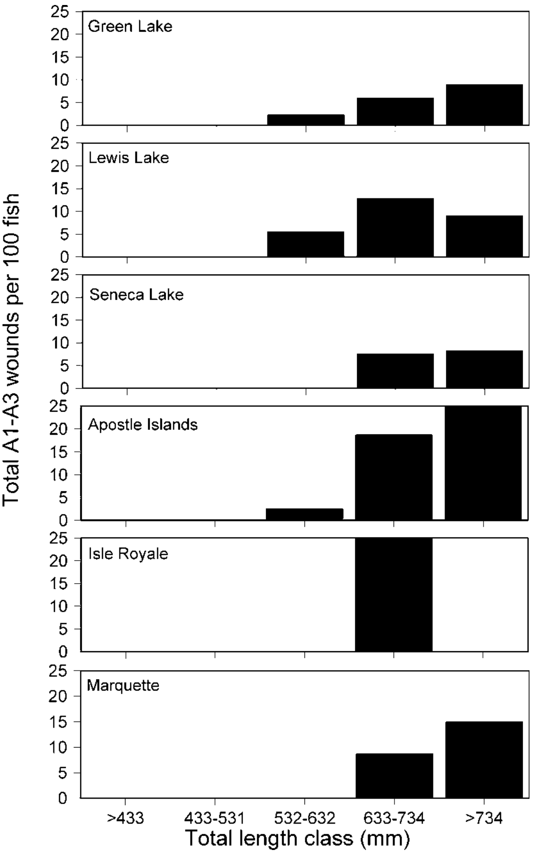

FIGURE 9.—Sea lamprey wounding (number of A1–A3 wounds per 100 fish) by length-class and strain of recaptured coded-wire-tagged lake trout from Lake Michigan, 1999–2000.

only onshore site stocked with coded-wire-tagged lake trout, 75% of the fish stocked there returned there, 19% were captured at offshore sites, and 6% at other onshore sites. In general, 84% of lake trout stocked at offshore sites as yearlings in spring returned to offshore sites in the fall, though many failed to return to their exact stocking site.

Dispersal radii varied among stocking sites and strains. For all fish and all sites combined, the dispersal radius at which 90% of the fish were recovered was 109 km but ranged from 24 km for fish stocked at Julian's Reef to 146 km for fish stocked at Boulder Reef (Figure 10a). Most strains (five of six) were recaptured within 85–112 km from where they were stocked, with the exception of the Apostle Islands strain that had the highest dispersal radius of 160 km (Figure 10b).

Discussion

Stocking of yearling lake trout at historically important spawning sites resulted in higher spawning aggregations than at unstocked sites. This result supports increasing the use of site-specific stocking for lake trout restoration. Catches of adults on unstocked, offshore reefs were low, with the exception of Waukegan Reef, and suggests that hatchery-reared lake trout have little ability to colonize these areas. Reestablishment of spawning aggregations at these sites could be accelerated through targeted stocking. Lake trout stocking in Lake Michigan (average = 2.7 million/year) has been significantly less than the 6–10 million fish recommended for restoration (Holey et al. 1995); however, increases in hatchery production to meet this demand are unlikely in the near future. Therefore, more strategic use of the limited hatchery production is warranted to increase spawner aggregations and the potential for reproduction at specific sites. Sites for future stocking should be selected based on habitat quality and protection from fishing (refuges) and sea lamprey mortality (offshore).

TABLE 3.—Percentages of coded-wire-tagged lake trout stocked as yearlings at eight sites and recaptured at a variety of sampling sites in Lake Michigan during 1999–2001. The numbers in parentheses refer to the sampling sites indicated in Figure 2.

	Stocking site							
Spawning site	Boulder Reef (42)	Clay Banks (3)	East Reef (6)	Gull Island Reef (43)	Julian's Reef (12)	Northeast Reef (7)	Richards Reef (38)	Sheboygan Reef (5)
Bay Harbor (31)	1.3			5.2			7.5	0.2
Big Reef (29)				1.3			0.8	
Boulder Reef (42)	35.4		0.4	18.7			10.4	
Cathead Bay (26)				1.3		0.4	0.8	
Clay Banks (3)	4.3	75.3	1.0	5.0	0.9	0.7	5.3	
East Reef (6)	0.7	2.1	50.2		4.1	40.7	3.5	30.8
Fisherman's Island (25)	14.3			11.1		0.7	24.6	
Fox Island, north (40)	0.7			0.8			2.0	
Fox Island, south (41)	2.1			2.5			2.0	
Good Harbor Reef (34)				1.0			0.6	
Green Can Reef (9)	2.3		12.0		2.2	10.2	0.8	12.6
Gull Island Reef (43)	12.4		0.3	20.1		0.3	7.3	
Head of Beaver (37)				1.1				
Ingall's Point (24)				2.9			4.6	0.2
Irishmen's Grounds (30)				1.7			1.0	
Jacksonport Reef (2)	0.7	16.7		1.7				
Julian's Reef (12)			1.4	1.1	22.1	7.8		3.9
Lee Point (21)	0.4						0.3	
Ludington Reef (15)			0.4	0.7	1.1	2.0	0.4	0.2
Menonaqua (32)	3.2	1.9	0.2	3.7			5.8	0.6
North Manitou Shoal (18)							0.5	
North Reef (20)			0.3	1.0			0.6	
Northeim Reef (4)	6.7	2.8	1.0	3.3		1.4	2.0	2.2
Northport–Cherry Home (23)				0.7			0.8	
Old Mission Point (22)				1.0			1.7	
Point Betsie Reef (17)	1.3			0.7		0.5	0.4	0.2
Port of Indiana (13)						0.4		1.0
Portage Point Reef (16)	2.9		1.0	3.3		2.0	4.0	0.8
Pt. Aux Barques (45)	4.8	1.3		5.1			8.6	
Richards Reef (38)	1.0							
South Milwaukee Reef (8)	0.9		2.5			2.8		2.3
Seven Mile Point Reef (28)	0.7			0.8				
Sheboygan Reef (5)			17.9	3.0	1.2	18.8	1.8	37.9
Trout Island Shoal (44)	1.9			1.1			1.3	
Waukegan Reef (11)	2.3		9.1		55.1	7.3	0.8	6.0
Waukegan Shore (10)			2.1		13.2	4.1		1.3
Percent offshore	74.5	18.8	93.9	64.3	84.7	88.6	56.7	93.3
Percent onshore	25.5	81.2	6.1	35.7	15.3	11.4	43.3	6.7

Variables other than low spawner abundance were also probably responsible for the lack of natural reproduction in Lake Michigan. Our results indicated that parental stocks of lake trout were relatively small, especially in northern Lake Michigan. Only 25% of the sites had spawner CPUEs near or above the mean level associated with wild recruitment elsewhere (Selgeby et al. 1995); however, 59% of the sites we sampled exceeded the minimum threshold for recruitment of 56 fish/km of net, and this suggests that factors other than adult abundance were limiting recruitment. For example, the spawner CPUE of a rehabilitated, mostly wild population at Gull Island Shoal, Lake Superior (Schram et al. 1995), has been over 450 fish/km of net lifted (S. Schram, Wisconsin Department of Natural Resources [WDNR], personal communication) in recent years. During years of decline and recovery, CPUEs at Gull Island Shoal exceeded 56 fish/km of net in only 3 of 19 years and ranged from 0.5 to 70.0 fish/km during 1951–1970. However, measurable reproduction (albeit low) occurred at Gull Island Shoal every year during 1951–1970 (Swanson and Swedberg 1980). Spawner abundances measured in Lake Michigan were well within the range observed at Gull Island Shoal during its recovery, which suggests that additional impediments must be preventing recruitment. Spawner abundances at Sheboygan and East reefs were similar to recent measures at Gull Island Shoal and therefore have highest probability for wild recruitment in the absence of other impediments. This suggests that high density is not the only prerequisite to initiate wild recruitment and highlights the need for a better understanding of recruitment bottlenecks in Lake Michigan.

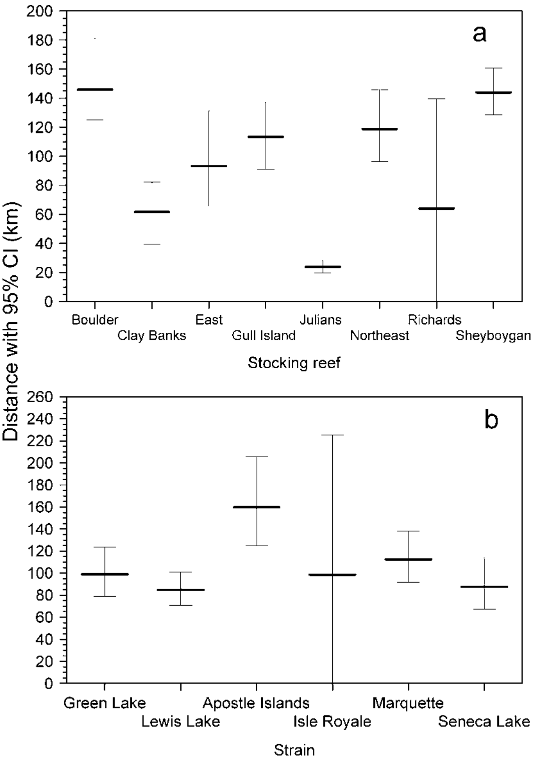

FIGURE 10.—Dispersal radii for 90% of the lake trout stocked at eight reefs in Lake Michigan. Panel **(a)** shows the data at particular sites for all strains and panel **(b)** the data for individual strains at all sites.

Low overall stock abundance in Lake Michigan is from low stocking rates in comparison with available physical (Dawson et al. 1997) and thermal habitat (Christie and Regier 1988) and excessive fishing in northern Lake Michigan in the past (Rybicki 1991; Holey et al. 1995; Hansen 1999; Modeling Subcommittee, Technical Fisheries Committee 2005). Sea lamprey populations have increased threefold since 2000 (Lavis et al. 2003; Great Lakes Fishery Commission, unpublished data) and have reduced adult numbers and potential egg deposition further (Modeling Subcommittee, Technical Fisheries Committee 2005). Although inadequate adult stocks and egg densities have been suggested as possible impediments to lake trout restoration (Eshenroder et al. 1984, 1999; Bronte et al. 2003; Jonas et al. 2005; Marsden et al. 2005), many other factors such as excessive predation on lake trout eggs and fry (Jones et al. 1995; Claramunt et al. 2005), stocking fish in areas with less favorable habitat (Bronte et al. 2003), and early mortality syndrome (EMS; Honeyfield et al. 2005a) have also been suggested. Early mortality syndrome occurs when lake trout consume alewives *Alosa pseudoharengus* that contain thiaminase, an enzyme that destroys thiamine in lake trout eggs and leads to mortality just before and at swim-up, and indirect mortality afterward. Alewives also may feed upon lake trout fry and impede recruitment (Krueger et al. 1995; Madenjian and DeSorcie 1999). Although the relative contributions of these aforementioned factors are unknown, all lead to a cumulative loss of reproductive potential that could be significant if initial eggs densities are low. Recent estimates at sites in northern Lake Michigan indicate egg depositions are 7 eggs/m^2 or less (Claramunt et al. 2005), and much lower than in other lakes with successful reproduction (Jonas et al. 2005). Low egg deposition in Lake Michigan makes the relative contribution of other recruitment bottlenecks difficult to assess because most hypotheses assume sufficient egg deposition and a single impediment mechanism, such as predation, is responsible. High adult abundances at some sites (i.e., Sheybogan Reef, East Reef) appear to have higher egg densities and produce some fry (J. Janssen, University of Wisconsin–Milwaukee, personal communication) but no older, wild fish have been detected; thus, other factors are limiting reproductive success. However, given the potential impact of other impediments, even higher spawning stock densities beyond thresholds discussed above may be required to compensate for the recruitment bottlenecks in Lake Michigan.

The recent detection of lake trout reproduction in Lake Huron, where spawner densities ranged from 48 to 60 fish/km (Inter-Tribal Fisheries and Assessment Program, unpublished data), support our contention that the spawner densities we observed in Lake Michigan should have produced some recruits. Wild age-0 lake trout were captured in bottom trawls throughout the main basin of Lake Huron for the first time in fall 2004 after more than 20 years of surveys (U.S. Geological Survey [USGS], unpublished data). Age-0 and age-1 wild fish were also caught throughout the lake in fall 2005 (J. Schaeffer, personal communication). Associated with the sudden onset in natural reproduction was a decline in sea lampreys and fishing mortality that increased the parental stock (Johnson et al. 2004) and the collapse of alewife populations (J. Schaeffer, USGS, personal communication). These occurrences may be responsible for the increased recruitment of wild lake trout as the result of increased egg deposition, a decline in EMS, and a reduction in lake trout fry predation by alewives.

Parental stocks of lake trout in Lake Michigan were young relative to reproducing populations elsewhere, and their age structure may limit the level of wild recruitment when other impediments exist. Old, large females produce more eggs than young, small females (Eschmeyer 1955; Peck 1988; Schram 1993; O'Gorman et al. 1998), and as age increases, a higher proportion of a cohort is mature. Lake trout can live well beyond 25 years (Behnke 1980; Martin and Olver 1980; Sharp and Bernard 1988; Burnham-Curtis and Bronte 1996; Schram and Fabrizio 1998). Spawning populations in undisturbed lakes are made often up of 15 or more age-groups, many fish being beyond the age at full cohort maturity (Mills et al. 2002). Parental stocks of rehabilitated populations in Lake Superior have mean ages of 12 years or older (Bronte et al. 2002; Schram 2005) and are made up of 20–25 age-groups compared to 5–15 age-groups in Lake Michigan. This longevity, combined with low fecundity relative to other species, necessitate the need for parental stocks composed of many age-groups. Although advanced ages of lake trout are rarely seen in Great Lakes populations under restoration (except in Lake Superior), longevity was certainly a feature of precollapse populations. Until recently, age composition has been overlooked in restoration efforts that track the progress of stocked fish under continued exploitation and sea lamprey predation. Although benchmarks for adequate spawner abundances have been developed (Selgeby et al. 1995) and applied here, failure to consider the age structure of the spawners limits its utility. However, the mean age of adult lake trout in northern Lake Huron that produced detectable recruitment in 2004 and 2005 was 6.7 years. Similarly, advanced adult ages were not needed to generate the limited natural recruitment observed on Six Fathom Bank in Lake Huron during spring 1994 (Madenjian et al. 2004), which suggests that in the absence of other recruitment impediments, advanced adult ages may not be required to initiate low levels of wild recruitment. However, sustained and substantial recruitment that will foster predominantly wild populations will probably require higher numbers of older adults than at present. Consideration of the sex ratio of spawners is also important, although it does not appear to be a problem in Lake Michigan as does overall adult abundance. Female spawners made up 25% of the all fish captured in this study and is similar to spawner aggregations of restored populations in Lake Superior (Schram 2005). The extended residency time on spawning reefs of males compared with females (Noakes and Curry 1995) accounts for sex ratios that never approach 1:1 during spawning surveys.

Survival differed among the strains stocked into Lake Michigan. The survival of the Seneca Lake strain was about three times that of the same year-classes (1985, 1989–1992) of Marquette and Lewis Lake fish. This superior survival of the Seneca strain is consistent with observations in Lakes Huron (Eshenroder et al. 1995b) and Ontario (Elrod et al. 1995) but differs from a recent analysis of two year-classes at the Sheboygan Reef, Lake Michigan (McKee et al. 2004), where Marquette fish survived better than Seneca Lake fish. Better survival of the Seneca Lake strain has been attributed to their ability to avoid sea lamprey attacks; however, the higher survival of Marquette fish at Sheboygan Reef occurred prior to age 3, when both strains were at a size less vulnerable to sea lampreys. Wounding rates at the Sheboygan Reef were much lower compared to those at Lakes Huron and Ontario; therefore, Marquette fish may survive as well as or better than Seneca Lake fish in the absence of sea lampreys (McKee et al. 2004). The Seneca Lake strain contributed more than expected to the parentage of 63 wild young-of-year lake trout collected in Little Traverse Bay (Page et al. 2003) based on stocking history. Older spawners, better survival of progeny, and higher postrelease survival of Seneca Lake fish have been suggested as possible explanations for their better reproductive success over other strains (Page et al. 2004). Higher survival, as mentioned above, through avoidance of sea lamprey predation, could explain the disproportionate contribution of Seneca Lake strain to recruitment, which makes any predictions of relative reproductive contribution based on stocking history alone tenuous. Contrary to Page et al. (2003), our results reinforce the unique utility of coded wire tags to evaluate lake trout strain performance, and their continued use in the restoration program is warranted.

Of the 137 coded-wire-tagged fish captured from the 1995–1997 year-classes of the Green Lake, Lewis Lake, Isle Royale, Apostle Islands, and Seneca Lake strains, only 9 of these were Isle Royale fish, which indicates very poor survival of this strain. Recoveries of these year-classes were low over the study period since these fish were just maturing into the adult population. This probably explains the lower overall survival of the 1995–1997 year-classes compared with that of the 1985, 1989–1992 year-classes (Figure 8); hence, any conclusions are tentative. However, a similar analysis of spring survey recaptures of younger fish in graded mesh gill nets (64–152-mm stretch measure) also indicated poor survival of the Isle Royale fish (Lake Michigan Lake Trout Task Group; unpublished data). Strains that have poor postrelease survival compared with those of others stocked (Isle Royale) or that have irreparable genetic issues (Green Lake strain; Kincaid et al. 1993; Krueger and Ihssen 1995) will be removed from the restoration program. The number of ecologically and genetically (Page et al. 2004) redundant shallow-water lean strains from Lake

Superior (Isle Royale, Apostle Islands, and Marquette) will be reduced to a single strain (i.e., Apostle Islands) for future stocking.

Sea lamprey wounding varied among some strains stocked into Lake Michigan; Apostle Islands fish had the highest wounding rates and Seneca Lake the lowest, but most differences were not statistically significant. The survival of Seneca Lake fish has been attributed to their ability to occupy cooler, and presumably deeper, water (Bergstedt et al. 2003), which results in less encounters with sea lampreys and higher probabilities of surviving an attack (Schneider et al. 1996). This may be the case, as well, in Lake Michigan. In Lakes Huron and Ontario, Seneca Lake fish had lower wounding than Marquette fish, which resulted in better survival (Eshenroder et al. 1995b; Schneider et al. 1996). The three Lake Superior strains stocked into Lake Michigan had high wounding rates for the largest size-classes (Figure 9), which implies that these strains may be more susceptible to sea lamprey attack. The Isle Royale strain had the lowest relative survival and high wounding, which suggests that this strain may be more affected by sea lamprey mortality than others. The Apostle Islands fish had the highest dispersal radius, which may account for their high wounding rate if these movements increased their exposure to sea lampreys. The results here must be approached with caution; most of the Lake Superior strains for the evaluation were stocked in northern Lake Michigan where sea lamprey wounding was highest, and conversely most Seneca Lake fish where stocked in the Southern refuge where wounding was the lowest. Therefore, it is difficult to separate strain and location effects.

Sea lamprey wounding varied by geographic area and has implications for restoration. Offshore areas in southern Lake Michigan appear to offer greater protection from sea lamprey predation than onshore areas. The highest probability for wounding for any comparison was for fish in onshore areas in northern Lake Michigan, where stocking should be avoided. Recently a large population of sea lamprey larvae was discovered above the lower dam on the Manistique River, a tributary to northern Lake Michigan (M. Fodale, U.S. Fish and Wildlife Service, personal communication). This population was reduced with lampricide treatments beginning in 2003. Estimates of spawning phase sea lamprey abundance in Lake Michigan declined coincident with these treatments and suggests that sea lampreys from this river had contributed to high wounding and degradation of lake trout stocks (Modeling Subcommittee, Technical Fisheries Committee 2005). Further and sustain control on these and other populations is required to rebuild lake trout parental stocks if restoration is to be achieved.

Recaptures of coded-wire-tagged lake trout suggest that fish return to the general area (i.e., reef complex) where they were stocked, but homing to specific spawning sites was less obvious. This is consistent with observations of hatchery-reared lake trout elsewhere (Eshenroder et al. 1984; Krueger et al. 1986; Bronte et al. 2002) and in contrast to a higher site fidelity apparent in wild fish (Krueger et al. 1986). Most fish returned to the general area near the stocking site, which is advantageous in areas such as the Northern and Southern refuges where multiple spawning sites occur in proximity. Fish that were stocked offshore tended to return to offshore sites to spawn. This is important because the most historically important spawning habitat is located offshore (Dawson et al. 1997), and fish stocked at these offshore sites are less vulnerable to sea lamprey predation (Table 2) and fishing.

The average dispersal distances of lake trout stocked at the eight stocking sites examined were generally low, averaging about 100 km (range = 24–146 km). The relative density and distribution of recapture sites can affect the dispersal results since not all lake areas are equally sampled; hence, the variation seen across stocking sites may be an artifact of the number of potential recapture sites in proximity. Recoveries of tagged and released adult lake trout in Lake Michigan and elsewhere indicated a wide range of dispersal distances (Schmalz et al. 2002), and our data fell within the range of previous observations. These distances are relatively modest given the size of Lake Michigan (length = 632 km; maximum width = 184 km), which is the sixth largest lake in the world by surface area. Only six fish (0.2%) of coded-wire-tagged lake trout recaptured were lake trout stocked into Lake Huron, and this demonstrates little immigration from Lake Huron during fall. Five out of the six strains examined had similar dispersal distances of about 100 km; however, Apostle Islands fish appeared to disperse more (150 km). Though our sample sizes were small for some strains, it appears that straying is a consistent feature of the biology of lake trout in large lakes (Kapuscinski et al. 2005), but the extent of dispersal can vary with stocking or tagging site, recapture strategy, and duration of the study. These observations are consistent with lake trout's ability to colonize new habitats and should not be viewed as problematic; however, hatchery-reared fish may have less capability than wild fish to find distance offshore sites as reported here.

The effectiveness of refuges in protecting lake trout from fishing is affected by the degree of straying. Schmalz et al. (2002), based on an estimated dispersal radius of 68 km for adults tagged at Clay Banks, suggested a 18,000-km^3 refuge was required to adequately protect lake trout from fishing. Our dispersal results from eight stocking sites suggest that about 30,000 km^2 or 51% of the lake would be required to accommodate the more extensive movements we observed. Expansion of refuge sizes required to protect more of the lake trout stocked within their boundaries may not be feasible. More uniform and restrictive harvest regulations among management units and states would be more practical for the protection of fish that leave the refuges (Schmalz et al. 2002).

Implications and Conclusions

Several prerequisites must be met for successful lake trout reproduction to occur. First, enough adult lake trout are needed to ensure sufficient egg densities to replenish the population. The adequacy of deposition is determined by the number and severity of life history bottlenecks that negatively affect recruitment. Secondly, eggs that are deposited must survive physical disturbance (Eshenroder et al. 1995a; Perkins and Krueger 1995), interstitial predation (Hudson et al. 1995; Jones et al. 1995; Claramunt et al. 2005; Jonas et al. 2005), and losses to EMS (Brown et al. 2005b; 2005c). Thirdly, eggs must hatch and the resulting fry must survive the latent effects of EMS (Fitzsimons et al. 1999) as well as additional predation (Krueger et al. 1995; Carl 2000; Ellrott and Marsden 2004). Due to local variations in the aforementioned conditions, the population requirements for successful reproduction may differ regionally; hence, the requisite densities of spawners will be determined by the variety and magnitude of recruitment bottlenecks. Further, spawner densities required to sustain broad geographic rehabilitation and support some level of fishing will probably need to be greater than those currently responsible for the recent reproductive success in Lake Huron. In Lake Superior, far lower numbers of lake trout spawners were required to initiate wild recruitment in the absence of alewives (Bronte et al. 1991), large standing stocks of interstitial predators, and the presence of remnant wild fish. In Lake Michigan, much higher parental stocks are probably required to overwhelm the “bottleneck gauntlet” to initiate and sustain significant wild recruitment.

Our results, combined with a recent analysis of other potential impediments to lake trout restoration in Lake Michigan (Bronte et al. 2003), will be used to develop recommendations for a new lake trout management plan to increase the probability of sustained natural reproduction in Lake Michigan. Recommendations will concentrate stocking in selected offshore areas with the best habitat that offers protection from fishing and sea lamprey mortality. Candidate areas will have numerous, closely aggregated reefs with suitable habitat, where the likelihood is highest that stocked fish will return and spawn. These approaches will probably result in higher initial densities of young fish, better survival probabilities to advanced ages, and higher egg deposition and reproductive potential. The resulting buildup of adult fish may also increase the potential for lake trout to exert community dominance through predation on local populations of egg and fry predators (Walters and Kitchell 2001). This could also alleviate the recruitment bottlenecks caused by EMS, where reductions in alewives through predation may increase the probability of adult lake trout ingesting native prey that could alleviate thiamine deficiencies (Brown et al. 2005a; Honeyfield et al. 2005b). With these steps we hope to reestablish self-sustaining stocks of Lake Michigan’s native predator that will augment the existing nonnative salmonine community.

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