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Recruitment Dynamics of the 1971–1991 Year-Classes of Lake Trout in Michigan Waters of Lake Superior

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Abstract.—In the 1950s, populations of lake trout *Salvelinus namaycush* in Lake Superior collapsed because of excessive exploitation and predation by sea lampreys *Petromyzon marinus*. Restoration began in the 1950s with the stocking of juvenile, hatchery-reared lake trout and controls on fisheries and sea lampreys. Partial restoration was declared in 1996 because wild fish made up most of the populations in many areas, especially in Michigan waters, so stocking was dramatically curtailed in most areas. We evaluated the production of age-7 lake trout (recruits) by age-8 and older wild and stocked parental lake trout (spawners). Using Ricker stock–recruitment models, we also evaluated the effects of large-mesh (114-mm stretch measure) gill-net effort on wild lake trout recruitment in Michigan waters of Lake Superior during 1970–1998. In general, the density of wild lake trout spawners increased, whereas that of stocked lake trout spawners decreased in all management areas investigated. The density of recruits was best described by the combined density of wild and stocked parents, which suggested similar reproductive contributions for both. Recruitment rates declined significantly with increasing spawner density in four of the five management areas and suggested that carrying capacities were reached and exceeded, which may serve as an indicator of population restoration. We conclude that both wild and stocked lake trout have contributed to the recruitment of lake trout in Michigan waters of Lake Superior. Large-mesh gill-net fishing effort varied in all Michigan management areas but did not account for the significant variation in wild lake trout recruitment. We conclude that levels of large-mesh gill-net fishing effort during 1970–1998 were not having an appreciable effect on wild lake trout recruitment in Michigan waters of Lake Superior.

Historically, lake trout *Salvelinus namaycush* were a dominant native predator and supported important commercial fisheries throughout the Great Lakes before their extirpation by 1960 from all the lakes except Lake Superior and Lake Huron, (Lawrie and Rahrer 1972, 1973). Lake trout in Lake Superior supported annual harvests of 0.75 × 10^6 kg in 1879, a peak harvest of 3.3 × 10^6 kg in 1903, and an average harvest of 2.0 × 10^6 kg during 1913–1950 (Baldwin et al. 1979). In Lake Superior, lake trout harvest was stable during 1913–1950, but yield was sustained in the 1940s in Michigan waters by increased fishing effort, while abundance declined (Hile et al. 1951). Sea lamprey *Petromyzon marinus* invaded Lake Superior in the 1940s and reached peak abundance around 1960 (Klar and Weise 1994). Lake trout stocks in Lake Superior, unable to sustain themselves in the face of intensive fishery exploitation and sea lamprey predation, collapsed by 1962 (Py-

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cha and King 1975; Pycha 1980; Swanson and Swedberg 1980).

Attempts to restore lake trout stocks in Lake Superior began in 1952, when stocks were declining, with the stocking of juvenile hatchery-reared lake trout (Lawrie and Rahrer 1972, 1973). Chemical control of sea lampreys was implemented in 1958, and by fall 1961 sea lamprey abundance had declined by 87% (Smith 1971; Smith et al. 1974). Commercial fisheries were closed in 1962 (Pycha and King 1975) but were reopened in Wisconsin in 1970 and in Michigan in 1980 as lake trout stocks increased from stocking and coincident with state and federal courts upholding Native American fishing rights (Hansen et al. 1995a). Stocking, sea lamprey control, and closure of fisheries allowed lake trout stocks to increase rapidly in the 1970s and 1980s (Pycha and King 1975).

An interagency plan for lake trout restoration in Lake Superior was developed during 1984–1986 that set a goal for sustainable lake trout yield of 2×10^6 kg/year; defined management areas; and set protocols for stocking, assessment, and reporting (LSLTTC 1986; Hansen et al. 1995a). The goal of the plan was to restore natural recruitment in optimal habitat areas of Lake Superior via stocking and reducing mortality from fishing and sea lampreys. In March 1996, after 35 years of intensive stocking, fishery managers declared victory in their pursuit of restoring natural recruitment of lake trout, and consequently, stocking was curtailed in most U.S. areas of Lake Superior (Hansen 1996). Thereafter, the lake trout restoration plan evolved into a management program that relied on harvest management of wild lake trout stocks.

Our first objective was to quantify the contribution of wild and stocked lake trout to catches of age-7 wild lake trout (hereafter, recruitment) in areas of Michigan waters of Lake Superior during 1970–1998. Previously, Hansen et al. (1997a) showed that stocked lake trout were largely responsible for recruitment in Michigan waters where wild lake trout stocks recovered after 1970. However, Hansen et al. (1997a) relied on average catch rates of all wild and stocked lake trout in assessment fisheries, rather than catch rates of specific age-classes, which may have confounded estimates of the contribution of wild and stocked lake trout to natural recruitment. Therefore, we developed year-class specific data for our analysis, to model the relative contributions of progeny of wild and stocked lake trout spawners to recruitment of specific year-classes. We expected that wild parents would contribute more to natural recruitment per individual because wild parents are generally thought to be more reproductively effective than stocked fish (Krueger et al. 1986; Schram et al. 1995).

Our second objective was to assess the effects of large-mesh gill-net fishing effort on wild lake trout recruitment in Michigan waters of Lake Superior. Previously, Hansen et al. (1996) found that declining density of stocked lake trout in Michigan waters was significantly associated with increasing large-mesh gill-net effort. Their analysis was based on the indexed survival of 1963–1982 year-classes of stocked fish and, thus, did not reflect the effect of gill-net fishing effort on year-classes of wild lake trout that recruited after 1982. Consequently, we analyzed data for more years (1970–1998) to include more recent year-classes (1971–1991) and to provide greater contrast in observed levels of gill-net fishing effort in relation to lake trout density. We focused on recruitment of wild lake trout because stocking was discontinued in Michigan waters in 1996. We expected that gill-net effort would be negatively related to wild lake trout density and that fishing mortality after the 45% reduction in gill-net fishing effort in Michigan waters of Lake Superior during 1990–1993 would not hinder sustainability of stocks (Hansen et al. 1995a).

Methods

Trends in relative abundance of lake trout were monitored with standardized gill-net surveys in five management areas in Michigan waters of Lake Superior: MI3, MI4, MI5, MI6, and MI7 (Figure 1). The management areas were designed to be similar in size to the range of lake trout movement in Lake Superior, based on studies that showed 90% of marked lake trout were recaptured within 80 km of release sites, regardless of their size at release or length of time at large (Eschmeyer et al. 1953; Buettner 1961; Pycha et al. 1965; Rahrer 1968; Swanson 1973; Ebener 1990; Peck and Schorfhaar 1991). Contracted commercial fisherman, Michigan Department of Natural Resources (MIDNR), and Chippewa-Ottawa Resource Authority (CORA) conducted the surveys using standard nets (114-mm stretched measure mesh, 210/2 multifilament nylon twine, 18 meshes deep, hung on the ½ basis) fished from late April through early June during 1970–1998 (Hansen et al. 1996). Nets were not all of the same length, so catch per effort (CPE) was defined as the number of fish caught per kilometer of net. Nets were fished for varying numbers of nights, so CPE was standardized to

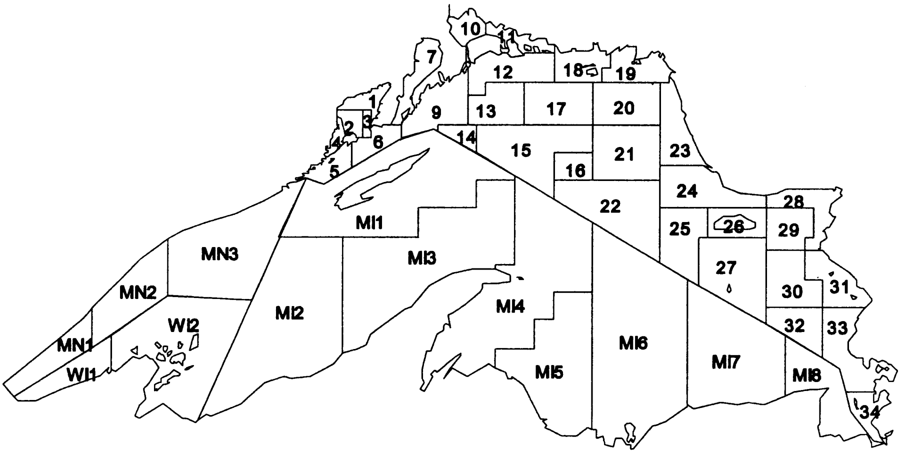

FIGURE 1.—Lake Superior lake trout management areas. The U.S. management areas are denoted by state: MI = Michigan; MN = Minnesota; WI = Wisconsin. Areas marked by numbers only are in Canada.

one net-night using conversions developed from gill-net saturation studies in 1995 (Hansen et al. 1998). The individual lift CPE of wild and stocked lake trout was transformed to natural logarithms, adding 1 to each CPE to adjust for zero catches: $\log_e(\mathrm{CPE} + 1)$. Mean $\log_e(\mathrm{CPE} + 1)$ and 95% confidence intervals were computed for each area and year and then back-transformed into geometric means and 95% confidence intervals (after subtracting 1).

Ages of wild fish were estimated by examining scale or otolith annuli from a random subsample of 20 fish per 2.54-cm length-class per management area. Length and age data were compiled into age-length keys within years and management areas, which were then applied to the length frequency for the entire catch within each area and year to determine age composition (Ricker 1975). All stocked lake trout were marked by removal of one or more fins before stocking in Lake Superior, so scale ages of hatchery fish were validated by matching the fin clip observed on individual fish to the year-class in which that fin clip was used (Hansen et al. 1994).

The geometric mean CPE of age-7 wild lake trout was used as an index of natural recruitment because selectivity analyses showed that lake trout were fully vulnerable to 114-mm assessment gill nets at age 8 (Hansen et al. 1997b). The CPE of age-8 and older wild and stocked lake trout were used to index spawning stock density because 50% of females reached sexual maturity by age 8 (Peck and Sitar 2000). To account for the time lag between spawning and recruitment at age 7, spawning stock CPE measured during 1970–1990 was matched with CPE of age-7 recruits during 1978–1998 to model recruitment of the 1971–1991 year-classes. Preliminary analyses indicated that average weights of spawning-age lake trout were the same for wild and stocked fish and did not change appreciably over time for all years for which weight data were available. Therefore, we defined stock size as CPE based on numbers rather than biomass, which allowed us to use data from all years and areas. Weight was measured for stocked and wild lake trout only during 1974–1975, 1989, 1991, 1994–1998. Analysis based on biomass would have severely limited the number of years included.

Stock–Recruitment

The contribution of progeny of wild and stocked lake trout to natural recruitment in Lake Superior was estimated using variants of the Ricker (1975) stock–recruitment model because lake trout are largely piscivorous and therefore probably regulate recruitment through cannibalism, as has been observed in Lake Superior (Martin and Olver 1980; Conner et al. 1993). The basic stock–recruitment model was

$$R = \alpha S e^{-\beta S},$$

where R is recruitment, S is the parental stock, α is the density-independent parameter that describes recruits per spawner at low parental stock sizes before density dependence, and β is the density-dependent parameter that describes the rate at which the stock–recruitment curve dampens as stock size increases. Based on a sequence of

TABLE 1.—Ricker stock–recruitment models for lake trout populations in Michigan waters of Lake Superior.

Model	Equation	Description
1	$R_i = \alpha_w W_i e^{-\beta_w W_i}$	Ricker stock–recruitment function based on wild parents
2	$R_i = \alpha_s S_i e^{-\beta_s S_i}$	Ricker stock–recruitment function based on stocked parents
3	$R_i = \alpha(W_i + S_i)e^{-\beta(W_i+S_i)}$	Ricker stock–recruitment function based on total stock size, i.e., wild and stocked parents combined
4	$R_i = \alpha(W_i + kS_i)e^{-\beta(W_i+kS_i)}$	Ricker stock–recruitment function based on total stock size and combined wild and stocked parents; *k* converts stocked fish into wild fish equivalents
5	$R_i = \alpha(W_i + kaS_i)e^{-\beta(W_i+kbS_i)}$	Ricker stock–recruitment function based on total stock size and combined wild and stocked parents. Density-dependent and density-independent terms apply to wild fish; different *k*s for density independence and density dependence: *ka* and *kb*
6	$R_i = (\alpha_W W_i + \alpha_S S_i)e^{-\beta_w W_i - \beta_s S_i}$	Ricker stock–recruitment function in which wild and stocked fish have their own density-independent and density-dependent terms

models developed by Hansen et al. (1997a), we modified the basic Ricker stock–recruitment model to include both wild (*W*) and stocked (*S*) parents and to allow for a constant equivalence of wild and stocked parents among different management areas (Table 1).

We assumed that recruitment rates and density dependence varied among management areas, based on Hansen et al. (1995a, 1997a). When fit to data from all management areas simultaneously, by use of indicator variables for each area, the models ranged in complexity from 10 parameters (model 1) to 20 parameters (model 6). Model 1 evaluated the contribution of wild parents only (*W*), model 2 evaluated the contribution of stocked parents only (*S*), and model 3 assumed that wild and stocked fish were equivalent ($W + S$; Table 1). Models 4–6 evaluated the relative contributions of wild and stocked parents. Models 4 and 5 included a parameter *k* that allowed stocked fish to be modeled as constant equivalents of wild fish. The parameter *k* was used as a way to parsimoniously describe the relative contribution of wild and stocked parents. Stocked fish were based on broodstock collected from Lake Superior, and natural recruits probably came from a mixed parentage. Therefore, wild and stocked lake trout could be some constant equivalent of one another, no matter where they lived and reproduced. Estimates for α and β could vary among management areas because habitat varied among management areas, but wild and stocked spawners may contribute comparably in all areas. Thus, the parameter *k* linked wild and stocked spawners to one another among management areas. Model 4 included one *k* for both density independence and density dependence, whereas model 5 included one *k* for density-independence (*ka*) and another for density-dependence (*kb*) for all areas. Model 6 allowed for different recruitment rates (α) for wild and stocked parents and for different density-dependence (β) for wild and stocked spawners in each management area.

Parameters and asymptotic standard errors were estimated numerically using a Gauss–Newton iterative algorithm and minimization of lognormal errors (Systat 1992). We used a variety of starting values for each model to ensure parameter estimates were not based on a local minimum sum of squares. Each time the number of parameters was increased, the model was evaluated to determine if the additional parameter(s) led to a lower scaled Akaike information criterion (AIC) and higher Akaike weight (Anderson et al. 2000). A scaled AIC allows for a ranking of the models being considered, such that larger scaled AIC values are less plausible than the lower ranked model (Anderson et al. 2000). Akaike weights can be used to assess the probability that the model is the best in the set of models being considered, in the sense that the least amount of information is lost by the model in approximating reality (Anderson et al. 2000). We chose AIC for model selection because all models we considered were not nested and were not therefore testable with likelihood-ratio tests. After model selection, model diagnostics were performed to test residuals for normality (residuals distributed in an approximately linear normal probability plot) and independence (residuals not autocorrelated, df = 94; $P > 0.05$).

We estimated peak recruitment and parental density that produced peak recruitment for the most parsimonious stock–recruitment model to illustrate how natural recruitment of lake trout differed among areas. Peak recruitment was estimated as $R_m = \alpha/\beta e$ for wild and stocked fish in each management area, where α was the density-independent parameter and β was the density-dependent parameter from the stock–recruitment model (Ricker 1975; Hilborn and Walters 1992). The parental density needed to produce peak recruitment was estimated for each management area as $P_m =$

$1/\beta$ where β was the density-dependent parameter from the stock–recruit model (Ricker 1975; Hilborn and Walters 1992).

Effective Fishing Effort

Commercial large-mesh gill-net fishing effort was examined as a source of mortality that may have limited natural recruitment, in addition to stock size and density dependence. Fishing mortality was indexed by commercial large-mesh gill-net fishing effort. Small-mesh gill nets were restricted to offshore, deepwater fisheries for chubs *Coregonus* spp. and inshore floating-net fisheries for lake herring *C. artedi*, both of which impose low mortality on lake trout (Hansen et al. 1995a). Trap nets were fished inshore but impose low mortality on lake trout (Schorfhaar and Peck 1993). To determine the amount of commercial large-mesh gill-net fishing effort that age-7 wild lake trout faced between hatching and recruitment, we weighted effort in years between spawning (age 0) and recruitment (age 7) using relative selectivity of 114-mm gill nets estimated by Hansen et al. (1997b): age 4 = 0.16, age 5 = 0.42, age 6 = 0.63, age 7 = 0.75, and age 8 = 1.00. Further, we assumed that only 33% of the commercial gill-net fishing effort was exerted from January to June, the same period when age-7 lake trout density in survey catches is indexed (M. P. Ebener, Chippewa-Ottawa Resource Authority, personal communication). Therefore, for recruitment indexed in any year, commercial large-mesh gill-net effort (i.e., 0.33) was multiplied by 0.75 in that year, by 0.63 for 1 year earlier, by 0.42 for 2 years earlier, and by 0.16 for 2 years earlier; these products were then summed to give the total effective effort faced during the previous 3.5 years. Effective commercial large-mesh gill-net fishing effort was added to each model of recruitment and evaluated in relation to all other models by using the scaled AIC ranking and likelihood statistic (Anderson et al. 2000).

Results

Relative Abundance

Density of natural lake trout recruits and wild parents generally increased during 1970–1998 in all Michigan management areas of Lake Superior, whereas density of stocked parents generally decreased (Figures 2–6). Parental stocks of hatchery origin were more numerous than those of wild origin during 1970–1985, and the reverse was true during 1986–1998. Wild parental CPE and natural recruitment CPE were generally very low early in the time series and increased as the origin of recruits moved away from stocking to natural reproduction. Natural recruitment CPE and wild parental CPE were highest in MI5 and MI6, and stocked parental CPE was highest in MI4 and MI5.

Stock Recruitment

Recruitment of age-7 wild lake trout during 1978–1998 was best described by density of age-8 and older wild and stocked parents during 1970–1990, wild and stocked parents being represented equally (model 3; Table 2). Errors were normally distributed and independent. Recruitment rates (α) ranged from 0.133 recruits/parent in MI4 to 0.803 recruits/parent in MI6 (Table 3). For all management areas except MI4, estimates of α were all significantly larger than their associated asymptotic standard errors (Table 3; $P \leq 0.05$), so recruits per unit of parental stock declined significantly with increased density in most Michigan management areas (Figure 7). In management area MI4 the estimate of α was not significantly larger than its associated asymptotic standard error ($P > 0.05$), so recruits per unit of parental stock did not decline significantly with increased density in that management area.

Stock–recruitment curves were shaped differently in each Michigan management area (Figure 7). The level of parental density that would produce peak recruitment was attained in all management areas for wild fish and stocked fish during 1970–1998, except MI4 (Table 4). Peak recruitment from the stock–recruitment function was lowest in MI3 and highest in MI4. The parental density that would produce peak recruitment from the stock–recruitment function was lowest in MI6 and highest in MI4.

Large-Mesh Gill-Net Effort

Effective fishing effort did not explain significant variation in recruitment beyond that explained by wild and stocked parents (Table 2). Effective fishing effort for the 1971–1991 year-classes was higher in MI4, MI6, and MI7 than in MI3 or MI5 (Table 5). In MI3, effective fishing effort increased from the 1984 to the 1987 year-classes, and then declined steadily from the 1988 to the 1991 year-classes. In MI4, effective effort steadily increased for the 1985 to the 1991 year-classes. In MI5, effective effort increased erratically for the 1981–1991 year-classes. In MI6, effective effort increased erratically for the 1980–1985 year-classes, and then declined to a lower level for the 1988–1991 year-classes. In MI7, effective effort in-

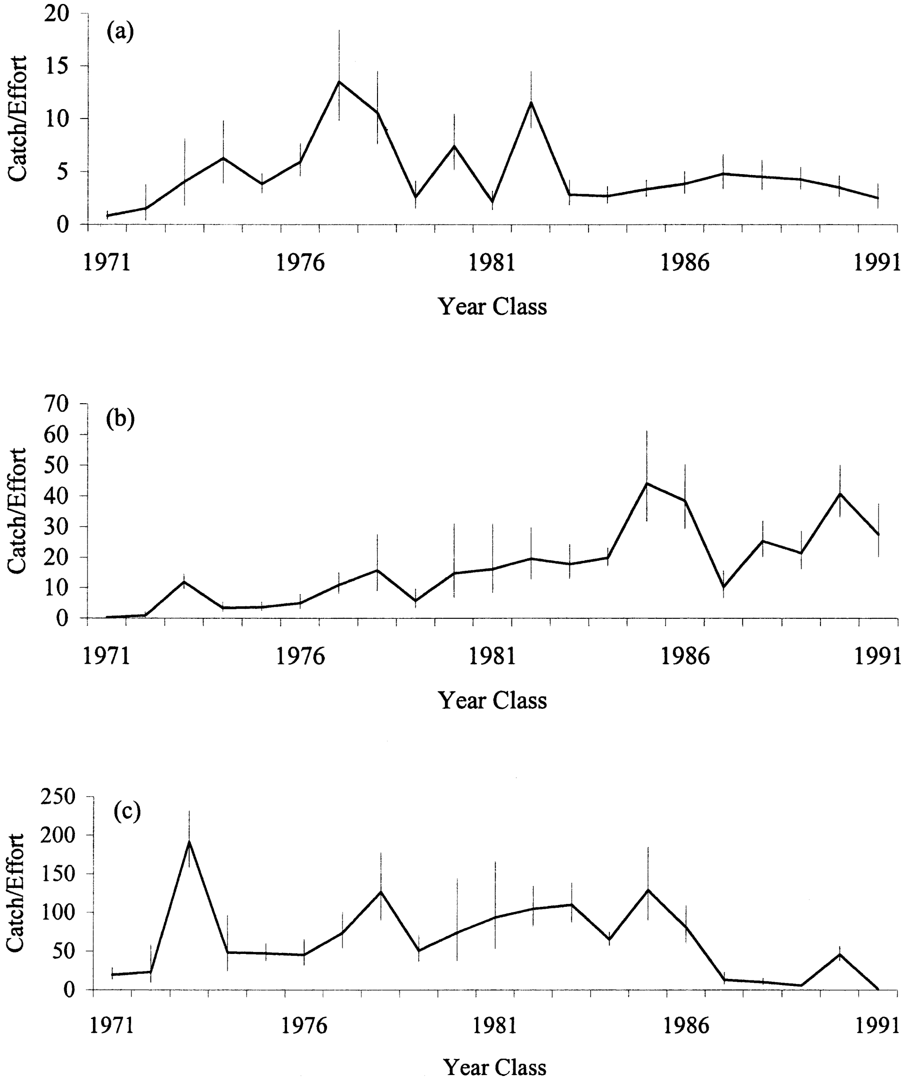

FIGURE 2.—Geometric mean catch per effort (CPE; fish · km^{-1} · net $night^{-1}$) of the 1971–1991 year-classes of lake trout in management area MI3 of Lake Superior for **(a)** age-7 natural recruits, **(b)** age-8 and older wild fish (parental stock), and **(c)** age-8 and older stocked fish (parental stock). The vertical lines denote 95% confidence intervals.

creased steadily from the 1981 to the 1991 year-classes.

Discussion

Relative Abundance

In general, wild lake trout abundance increased and stocked lake trout abundance decreased during 1970–1998. Previous reports of lake trout abundance in the 1970s and 1980s indicated that stocked fish were increasing and wild fish were rare (Lawrie and Rahrer 1973; Lawrie 1978; MacCallum and Selgeby 1987; Hansen et al. 1995a, 1995b). Our results indicate that wild lake trout were more abundant than stocked lake trout during the 1980s, which was also reported by MacCallum and Selgeby (1987), Peck and Schorfhaar (1994), and Hansen et al. (1995a). Our results show that wild lake trout abundance increased slightly or fluctuated without trend in the 1980s and 1990s and that stocked fish became rare over the same period, as also indicated by Peck and Sitar (2000). Wild lake trout now compose over 80% of populations in all Michigan areas (Peck and Sitar 2000).

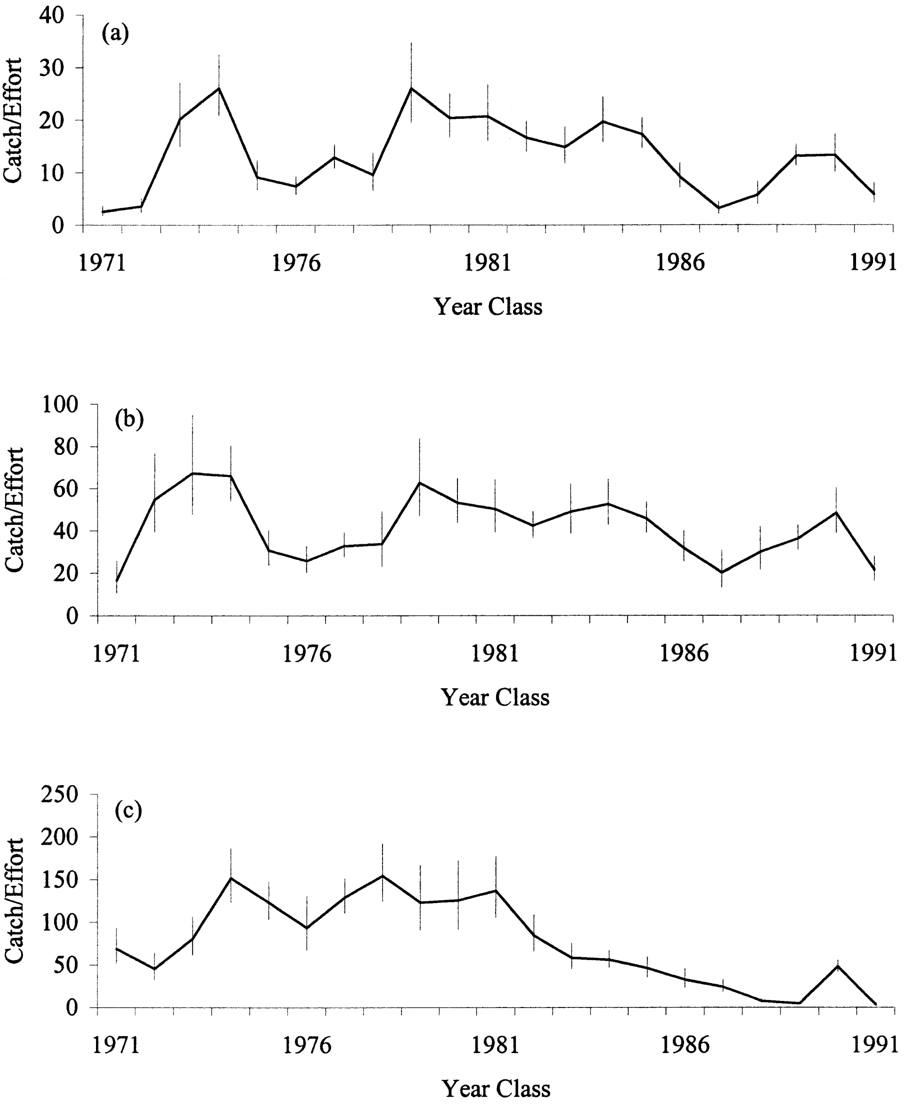

FIGURE 3.—Geometric mean catch per effort (CPE; fish · km^{-1} · net night^{-1}) of the 1971–1991 year-classes of lake trout in management area MI4 of Lake Superior for **(a)** age-7 natural recruits, **(b)** age-8 and older wild fish (parental stock), and **(c)** age-8 and older stocked fish (parental stock). The vertical lines denote 95% confidence intervals.

Stock Recruitment

Our results suggest that wild and stocked lake trout had similar recruitment rates in Michigan waters of Lake Superior during 1970–1990, in contrast to Hansen et al. (1997a), who found that stocked lake trout reproduced at near-replacement rates and that wild lake trout reproduced at 10% or less of replacement levels. Our findings may differ from Hansen et al. (1997a) for two reasons. First, Hansen et al. (1997a) relied on average CPE of all ages of fish, lagged 8 years between spawning and recruitment, whereas our analysis used average CPE of age-7 recruits and age-8 and older adults. Stock–recruitment parameters are estimated more accurately when based on age-specific data (Hilborn and Walters 1992), so Hansen et al. (1997a) were more likely to fail to accurately estimate stock–recruitment parameters because they did not use age composition data. Second, Hansen et al. (1997a) focused on the 1960–1986 year-classes, when wild lake trout densities were lower, whereas we relied on the 1971–1991 year-classes,

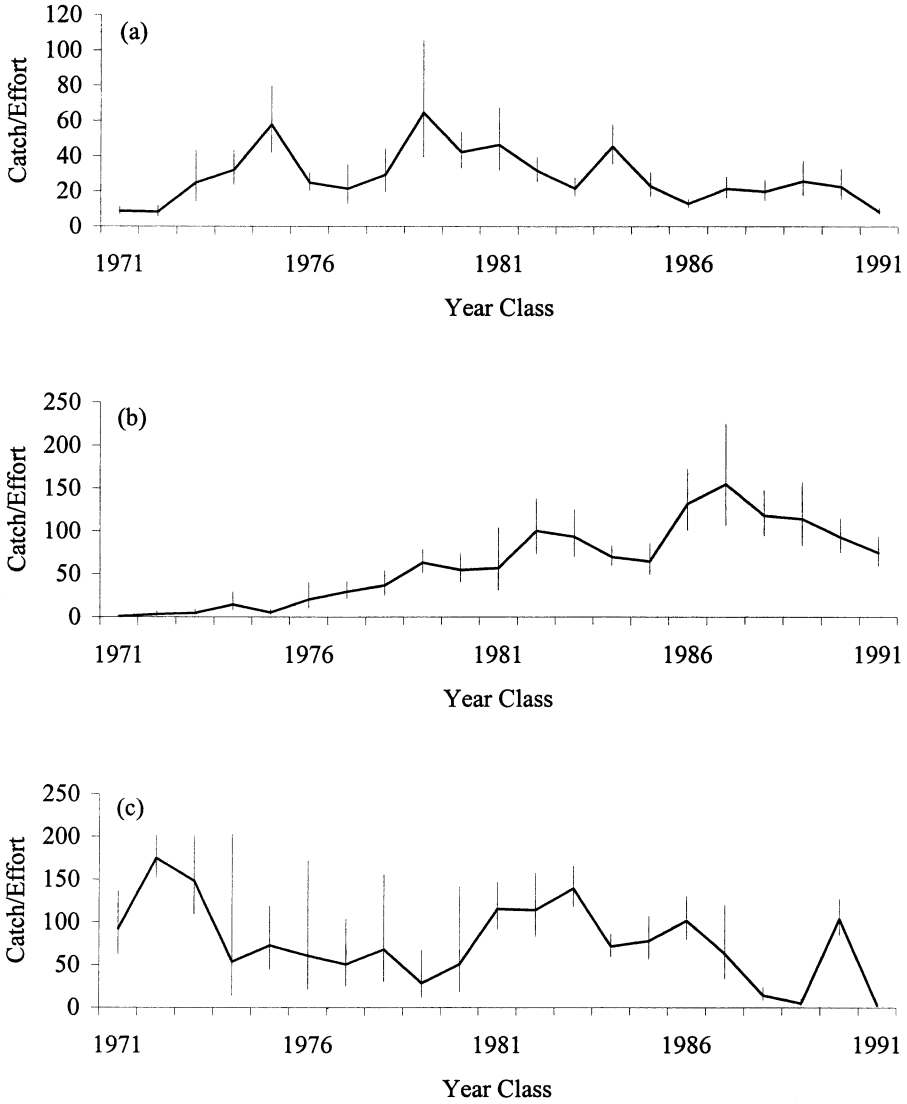

FIGURE 4.—Geometric mean catch per effort (CPE; fish · km^{-1} · net $night^{-1}$) of the 1971–1991 year-classes of lake trout in management area MI5 of Lake Superior for **(a)** age-7 natural recruits, **(b)** age-8 and older wild fish (parental stock), and **(c)** age-8 and older stocked fish (parental stock). The vertical lines denote 95% confidence intervals.

when wild lake trout densities were greater. Stock–recruitment parameters are estimated more accurately when data cover a broad range of spawner densities (Hilborn and Walters 1992); therefore, Hansen et al. (1997a) were more likely to fail to accurately estimate stock–recruitment parameters because they relied on data over a period when the range of wild lake trout density was less than during the period covered by our analysis.

Walters et al. (1980) suggested that stocked fish should be as reproductively successful as wild fish for maintaining progress toward lake trout recovery, as we found in our analyses of lake trout in Michigan waters of Lake Superior. Peck (1986) reported that fecundity of hatchery and wild lake trout was similar. However, Krueger et al. (1986) found that wild adult lake trout produced significantly greater numbers of recruits in the Apostle Islands region of Lake Superior because stocked fish were less able to locate offshore spawning reefs and shoals and, therefore, were reproductively less effective than wild lake trout. Results

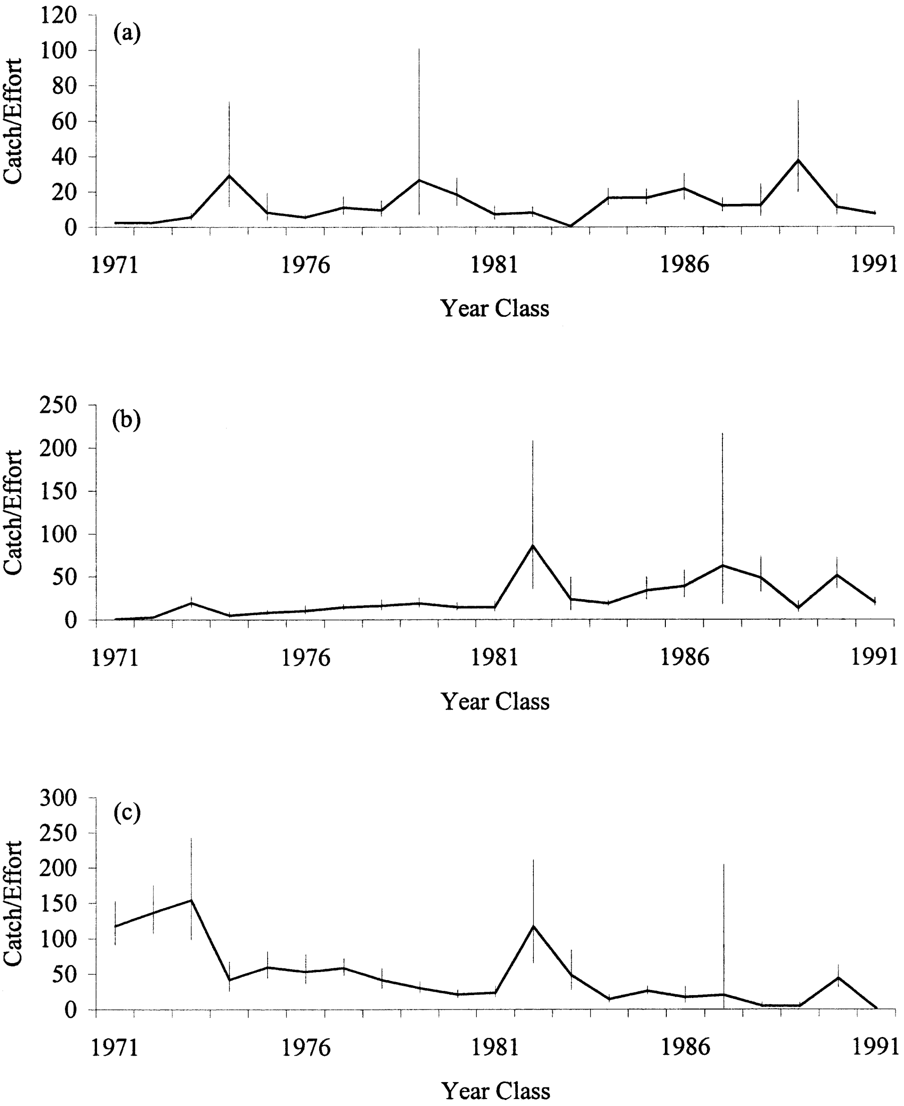

FIGURE 5.—Geometric mean catch per effort (CPE; fish · km^{-1} · net night^{-1}) of the 1971–1991 year-classes of lake trout in management area MI6 of Lake Superior for **(a)** age-7 natural recruits, **(b)** age-8 and older wild fish (parental stock), and **(c)** age-8 and older stocked fish (parental stock). The vertical lines denote 95% confidence intervals.

from a tagging experiment indicated that spawning site fidelity was 100% for native lake trout on Gull Island Shoal but only 58.6% for hatchery-origin lake trout returned to the spawning grounds (Swanson 1973); wild spawners at this site were the major source of recruitment (Schram et al. 1995; Hansen et al. 1997a). Similar evidence of lack of homing by hatchery fish has been observed elsewhere (Bronte et al. 2002). The inability of hatchery fish to home in on optimal spawning areas greatly reduces their spawning potential (Swanson 1973). In Michigan waters of Lake Superior, where spawning habitat is widely distributed inshore, hatchery-origin lake trout may locate and use suitable spawning habitat more easily than in Wisconsin waters of Lake Superior, where spawning habitat is mostly distributed offshore.

Our analyses indicated that lake trout density in four of five Michigan management areas (MI3, MI5, MI6, MI7) was high enough to exhibit density dependence. Bronte et al. (1995) suggested that evidence of density-dependence in recruit-

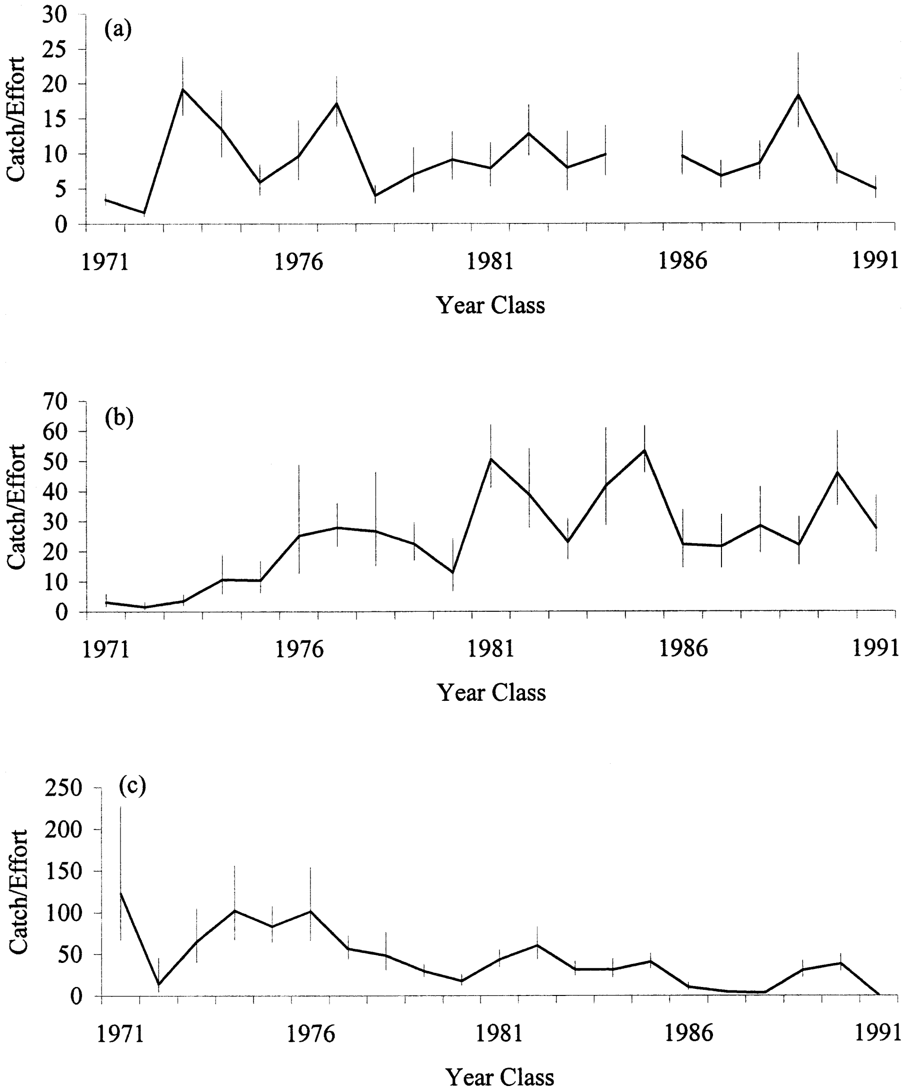

FIGURE 6.—Geometric mean catch per effort (CPE; fish · km^{-1} · net night^{-1}) of the 1971–1991 year-classes of lake trout in management area MI7 of Lake Superior for **(a)** age-7 natural recruits, **(b)** age-8 and older wild fish (parental stock), and **(c)** age-8 and older stocked fish (parental stock). The vertical lines denote 95% confidence intervals.

ment could be used as an indicator of restoration in lake trout populations, once natural reproduction was advanced. Hilborn and Walters (1992) described density dependence as a compensatory change in reproduction, where the number of recruits per spawner decreases as stock size increases, as evident in our results. Declining trends in average length at age of lake trout in some areas of Michigan waters of Lake Superior (Peck and Schorfhaar 1994; Peck and Sitar 2000) may be another indicator of density-dependence. Evans and Willox (1991) examined lake trout stock–recruitment relationships in several small inland Ontario lakes and found that density-dependent cannibalism limited recruitment. In Lake Superior, lake trout cannibalism has been observed (Conner et al. 1993; S. Sitar, Michigan Department of Natural Resources, unpublished data). Limited availability or saturation of spawning habitat in Lake Superior has also been suggested (Bronte et al. 1995) as a mechanism for compensatory change in recruitment. Wilberg et al. (2003) reported that

TABLE 2.—Comparison of Ricker models for describing recruitment of lake trout in Michigan waters of Lake Superior as a function of wild (*W*) and stocked (*S*) parents and large-mesh gill-net fishing effort. The parameter *k* converts stocked fish into wild fish equivalents. The models are ranked in order of the scaled Akaike information criterion (AIC). Akaike weight refers to a weighted AIC that can be interpreted as the probability that the model is the best one in the set of models considered; MSE = mean square error.

Model	Parameter	df	MSE	AIC	Scaled AIC	Akaike weight
Model 3: (*W* + *S*)	10	94	0.319	−87.458	0.000	0.813
Model 4: *W*, *S*, 1*k*	11	93	0.321	−83.605	3.853	0.118
Model 5: *W*, *S*, 2*k*	12	92	0.317	−81.710	5.749	0.046
Model 1: *W* only	10	94	0.345	−80.161	7.297	0.021
Model 3 + gill nets	15	89	0.315	−72.811	14.647	<0.001
Model 4 + gill nets	16	88	0.308	−71.634	15.825	<0.001
Model 5 + gill nets	17	87	0.311	−67.613	19.846	<0.001
Model 2 + gill nets	15	89	0.336	−67.067	20.391	<0.001
Model 1 + gill nets	15	89	0.340	−66.014	21.444	<0.001
Model 6: *W*, *S*	20	84	0.296	−62.392	25.066	<0.001
Model 2: *S* only	10	94	0.465	−51.960	35.498	<0.001
Model 6 + gill nets	30	79	0.294	−36.710	50.749	<0.001

lake trout abundance in most Michigan management areas was higher during 1929–1943 than at any other time during the period evaluated, up until 1984–1998. This may explain our results that indicate lake trout stocks are now experiencing density-dependent survival in MI3, MI5, MI6, and MI7. The range of observed CPE in MI4 was similar to that found in other areas, but was not high enough to exhibit density-dependence for reasons that are not clear. Schram et al. (1995) also found that the lake trout population at Gull Island Shoal, Wisconsin, was not affected by density-dependent survival during 1964–1992. However, the lake trout population on Gull Island Shoal did not recover as rapidly as those inshore, probably because of fishery exploitation in adjacent areas throughout its recovery period, and therefore, density had probably not reached that needed for peak recruitment.

Large-Mesh Gill-Net Effort

Our results suggest that large-mesh gill-net fishing was not a significant factor limiting recruitment of the 1971–1991 year-classes of wild lake trout in five different areas of Michigan waters of Lake Superior, which contrasted to Hansen et al. (1996), who found that large-mesh gill-net fishing effort was negatively related to recruitment of the 1963–1982 year-classes of stocked lake trout in Michigan and Wisconsin waters of Lake Superior. Our results may have differed from those of Hansen et al. (1996) for several reasons. First, we analyzed the effect of fishing mortality on wild recruitment, whereas Hansen et al. (1996) analyzed the effect of fishing mortality on stocked recruit-

TABLE 3.—Stock–recruitment parameter estimates (model 3) for wild and stocked lake trout in five Michigan management areas of Lake Superior (see Figure 1) during 1970–1998. Asymptotic standard errors (ASE) are reported for the model estimates.

Management area	α	ASE	β	ASE
MI3	0.138	0.042	0.010	0.003
MI4	0.133	0.046	0.001	0.003
MI5	0.664	0.233	0.009	0.002
MI6	0.803	0.215	0.022	0.003
MI7	0.348	0.114	0.014	0.004

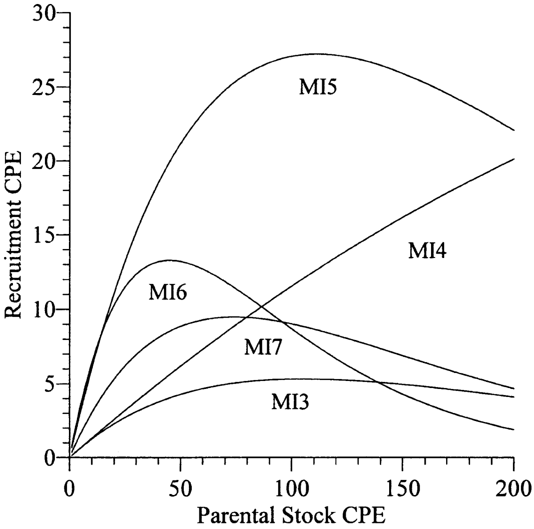

FIGURE 7.—Relationships between numbers (i.e., catch per effort [CPE]) of recruits and parental stocks of lake trout in five management areas in the Michigan waters of Lake Superior during 1970–1998.

TABLE 4.—Recruitment estimates for wild and stocked lake trout in five management areas in Michigan waters of Lake Superior during 1970–1998. R_m designates the level of peak recruitment catch per effort (CPE, $\alpha/\beta e$) and P_m designates the level of parental CPE that produces peak recruitment ($1/\beta$). The CPE was the geometric mean number of fish caught per kilometer of net per night (normalized by a $\log_e(x + 1)$ transformation and then back-transformed).

Management area	$R_m = \alpha/\beta e$	$P_m = (1/\beta)$
MI3	5.328	104.906
MI4	35.439	726.588
MI5	27.221	111.175
MI6	13.292	44.980
MI7	9.486	74.037

ment. Second, we weighted gill-net fishing effort according to the relative selectivity of the gear for each prerecruit age of wild lake trout, whereas Hansen et al. (1996) weighted effort equally in all years between stocking and recruitment to age 7. Lake trout have low selectivity to large-mesh gill nets before age 4 and become increasingly vulnerable to capture, from age 4 to age 8 (Hansen et al. 1997b), so large-mesh gill-net fishing effort is most likely to influence survival in the 2–3 years before their recruitment to age 7. Third, we analyzed recruitment of wild lake trout in five different areas of Michigan waters of Lake Superior, whereas Hansen et al. (1996) analyzed recruitment of stocked lake trout across more areas of Michigan waters of Lake Superior. The different spatial scales of the two analyses may partly explain differences in the findings, in addition to the other differences in the two analyses noted above.

We included the 1971–1991 year-classes of lake trout (captured at age 7 in 1978–1998) that were fully vulnerable to reduced commercial large-mesh gill-net fishing effort, whereas Hansen et al. (1996) included the 1963–1986 year-classes of lake trout (captured at age 7 in 1970–1993) that were not vulnerable to reduced commercial effort. It was movement of tribal fishing operations to other Great Lakes or outside Michigan waters that reduced gill-net effort by 45% during 1990–1993 (M. P. Ebener, Chippewa-Ottawa Resource Authority). Inclusion of year-classes that were vulnerable to reduced commercial gill-net fishing effort, which reflect increased contrast in effective effort, would increase the likelihood that we more accurately estimated the effect of fishing effort on lake trout recruitment than was possible for Hansen et al. (1996). We do note that if fishing mortality were having a significant effect on survival of stocked fish, increased recruitment of wild fish would have been unlikely because both wild and hatchery fish were subjected to the same gill-net fishery (see Ebener and Bronte 1986).

Management Implications

We found that stocked and wild lake trout both contributed to restoring self-sustaining stocks in Lake Superior, which was the primary objective of all fishery management agencies involved with lake trout rehabilitation in the Great Lakes. Naturally reproducing lake trout stocks have been reestablished throughout much of Lake Superior, and wild recruitment has been observed in Lake Ontario during 1995–2002 (Robert O'Gorman, U.S. Geological Survey, personal communication), where parental stock sizes of hatchery-reared trout are high. In most other areas of the Great Lakes, however, natural reproduction is limited or nonexistent. Considerations to rehabilitate or maintain stocks through stocking must first evaluate habitat where fish are to be stocked. In areas that contain abundant inshore habitat, hatchery fish may be as reproductively effective as wild fish, whereas in areas that contain mostly offshore habitat, hatchery fish may not be as reproductively effective as wild fish.

We found that large-mesh gill-net fishing effort did not explain significant variation in recruitment of wild lake trout to age 7, so we conclude that levels of gill-netting effort in the 1990s were not hindering lake trout recruitment. However, we did not evaluate the effect of large-mesh gillnet fishing effort on survival of lake trout after age 7 or on hatchery fish, which were the subject of earlier studies (Hansen et al. 1995b, 1996). Remembering the relation of gill netting to the lake trout collapse of the 1950s (Pycha and King 1975), commercial fisheries should continue to be monitored and regulated in Lake Superior to ensure that levels of large-mesh gill-net effort do not diminish lake trout survival beyond age 7. Lake trout abundance and mortality should continue to be monitored in all Michigan management areas, to verify that stock density and survival remain within limits ensuring that wild lake trout stocks will be robust and sustained in the future.

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TABLE 5.—Effective commercial large-mesh (114 mm stretch measure) gill-net fishing effort (km) in five management areas in Michigan waters of Lake Superior for the 1971–1991 lake trout year-classes. A zero in an area indicates that effort was negligible in that year.

	Management area				
Year-class	MI3	MI4	MI5	MI6	MI7
1971	0.000	0.000	0.000	0.000	0.000
1972	0.000	0.000	0.000	0.000	0.000
1973	0.000	0.000	0.000	0.000	0.000
1974	0.000	0.000	0.000	0.000	0.000
1975	0.000	0.000	0.000	0.000	0.000
1976	0.000	0.000	0.000	0.000	0.000
1977	0.000	0.000	0.000	0.000	0.000
1978	0.000	0.000	0.000	0.000	0.000
1979	0.000	0.000	0.000	0.000	0.000
1980	0.000	0.000	0.000	34.777	0.000
1981	0.000	0.000	1.494	202.570	65.925
1982	0.000	0.000	4.632	537.799	212.876
1983	0.000	0.000	21.643	1,010.124	339.474
1984	37.794	0.000	73.292	1,436.868	527.789
1985	270.141	102.767	99.774	1,480.504	868.786
1986	720.224	629.071	64.255	1,324.521	1,484.552
1987	936.218	1,362.751	58.903	1,134.246	1,857.538
1988	772.030	1,764.630	96.149	1,028.087	2,006.608
1989	598.963	2,281.646	112.371	1,021.342	2,116.861
1990	434.535	2,719.334	119.407	1,039.843	2,461.244
1991	382.870	2,909.694	145.197	1,027.395	2,849.007

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