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Historic and Modern Abundance of Wild Lean Lake Trout in Michigan Waters of Lake Superior: Implications for Restoration Goals

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Abstract.—Populations of lake trout *Salvelinus namaycush* in Lake Superior collapsed in the late 1950s due to overfishing and predation by sea lampreys *Petromyzon marinus*. A binational effort to restore the lean morphotype of lake trout began with the stocking of hatchery-reared fish followed by the chemical control of sea lampreys and closure of the commercial fishery. Previous comparisons of the contemporary abundance of wild lean lake trout with that from historic commercial fishery statistics indicate that abundance was higher historically. However, this conclusion may be biased because several factors—the inclusion of siscowet (the ‘‘fat’’ morphotype of lake trout) in the catch statistics, the soak time of nets, seasonal effects on catch per effort, and the confounding effects of effort targeted at lake whitefish *Coregonus clupeaformis*—were not accounted for. We developed new indices of historic lean lake trout abundance that correct for these biases and compared them with the assessment data from 1984 to 1998 in Michigan waters of Lake Superior. The modern (1984–1998) abundance of wild lean lake trout is at least as high as that during 1929–1943 in six of eight management areas but lower in one area. Measures to promote and protect naturally reproducing populations have been more successful than previously realized.

Historically, lake trout *Salvelinus namaycush* were the predominant piscivore in Lake Superior (Lawrie and Rahrer 1972). These lake trout have differentiated into many discrete and semidiscrete stocks that use different habitats, both temporally and spatially (Goodier 1981). Three morphotypes are recognized in Lake Superior: the lean morphotype, the siscowet or ‘‘fat’’ morphotype, and the humper or banker morphotype (Khan and Qadri 1970; Lawrie and Rahrer 1973; Pycha and King 1975; Moore and Bronte 2001). In spring, lean lake trout usually inhabit waters shallower than 80 m (Dryer 1966; Selgeby and Hoff 1996), siscowet lake trout usually inhabit waters deeper than 60 m (U.S. Geological Survey [USGS], Great Lakes Science Center, unpublished data), and humper lake trout inhabit isolated offshore reefs (Eschmeyer and Phillips 1965; Rahrer 1965).

During 1913–1950, the annual lake trout yield of Lake Superior was relatively stable and averaged 2.0 million kg (Hile et al. 1951; Baldwin et al. 1979; Hansen et al. 1995b). In the late 1950s, lake trout populations collapsed to near extinction because of overfishing and predation by sea lampreys *Petromyzon marinus* (Lawrie and Rahrer 1972; Pycha and King 1975; Hansen et al. 1995a). Stocking of hatchery-reared lean lake trout began in 1952 (Lawrie and Rahrer 1972), and chemical control of sea lampreys began in 1958 with treatments in larval nursery areas in streams (Smith and Tibbles 1980). Commercial lake trout fisheries were closed in the summer of 1962, when the sea lamprey abundance had been reduced 87% in Lake Superior and stock rebuilding seemed possible (Pycha and King 1975). Lake trout restoration has focused mainly on the lean morphotype, but the siscowet and humper morphotypes have also benefited from reduced fishing and sea lamprey mor-

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tality. During the 1960s, the abundance of hatchery-reared lean lake trout increased greatly; 95% of the lake trout caught inshore were of hatchery origin (Lawrie and Rahrer 1972). The abundance of wild lean lake trout increased in the 1970s and early 1980s but declined somewhat during the late 1980s and 1990s (Hansen et al. 1995b).

Millions of dollars have been spent on lake trout restoration and progress has been promising, with natural reproduction occurring throughout most of Lake Superior (Hansen et al. 1995a). The current objective for lake trout management on Lake Superior is to

> Achieve and maintain genetically diverse self-sustaining populations of lake trout that are similar to those found in the lake prior to 1940, with lean lake trout being the dominant form in near-shore waters, siscowet lake trout the dominant form in offshore waters, and humper lake trout a common form in eastern waters and around Isle Royale (Horns et al., in press).

However, this management objective is not an easily quantifiable standard for lake trout restoration.

Progress toward the restoration of lean lake trout in Michigan waters of Lake Superior was determined by Hansen et al. (1995b) by comparing the contemporary relative abundance of these fish, indexed as catch per effort (CPE; number per kilometer of gill net set for 1 night) in spring assessment fisheries, with the historical relative abundance, indexed as large-mesh (≥114 mm [stretch measure]) gill-net CPE during 1929–1943. Hansen et al. (1995b) showed that the abundance of wild lean lake trout had not yet reached historical levels in most Michigan waters, but their analysis may have been biased for four reasons. First, they assumed that all of the historic catch was of the lean morphotype. This was incorrect, because siscowet lake trout were known to compose a portion of the catch (Pycha and King 1975; Hansen et al. 1995b) and would bias the historical CPE of the lean morphotype upwards. Second, historical and contemporary data collection methods differed. Annual indices of historical lake trout abundance were derived from cumulative commercial catch and effort data that were collected over most of the year with multiple gears. By contrast, indices of contemporary abundance were based on collections during late April–early June with only one type of gear, 114-mm gill nets (Pycha and King 1975; Pycha 1980; Hansen et al. 1995a). Any seasonal bias (Sakagawa 1967) or gear selectivity (Hansen et al. 1997b) would affect the comparability of CPE in the two periods. Third, Hansen et al. (1995b) used a linear relationship to link the historical commercial fishery time series with the assessment time series, which overlapped during 1959–1961. This may not have been appropriate because fishing conditions during 1959–1961 were different from those during 1929–1943. Commercial fishermen fished their nets fewer nights during 1959–1961 than during 1929–1943 (USGS, Great Lakes Science Center, unpublished data), and lake trout were unusually small because of intense sea lamprey predation during 1959–1961 (Pycha and King 1975). Lastly, any historic effort that caught a lake trout was considered to have been targeted at lake trout (Hile 1962), but fishing effort directed at lake whitefish *Coregonus clupeaformis* may have confounded indices of lake trout abundance derived from mixed catches of both species (Eshenroder 1992).

Given these potential problems, a more accurate comparison between historical and current indices of relative abundance is needed. Our objectives were to develop a more accurate index of historic abundance that was corrected for season, soak time, morphotype composition, and targeted effort and to compare this index with contemporary assessment data. Using the revised index, we sought to determine how far lake trout restoration has proceeded in Michigan waters of Lake Superior.

Methods

Commercial and assessment fishery data.—Historical commercial catch reports from 1927 to 1961 are archived on microfiche transparencies at the Great Lakes Science Center, Ann Arbor, Michigan. We extracted the lift-specific information on the lake trout fishery from monthly commercial fishing reports to develop a database that was more comparable to contemporary assessment data. Before 1929, the data were incomplete and inaccurate, but by 1929 they were deemed to be adequate for statistical analyses (Hile 1962). Fishing locations, especially those beyond 5 km from port, were rarely recorded as recognizable site names but rather given as compass bearings and running times from the ports of origin. Therefore, we approximated fishing locations by running the reported course on National Oceanic and Atmospheric Administration charts at an assumed cruising speed of 14.8 km (8 nautical miles) per hour for fishing vessels. At the end of each course, we noted the fishing depth (which was not reported) on the chart and assigned the catch and effort to a statistical grid of 10′ latitude × 10′ longitude. Because the catch report forced lean and siscowet

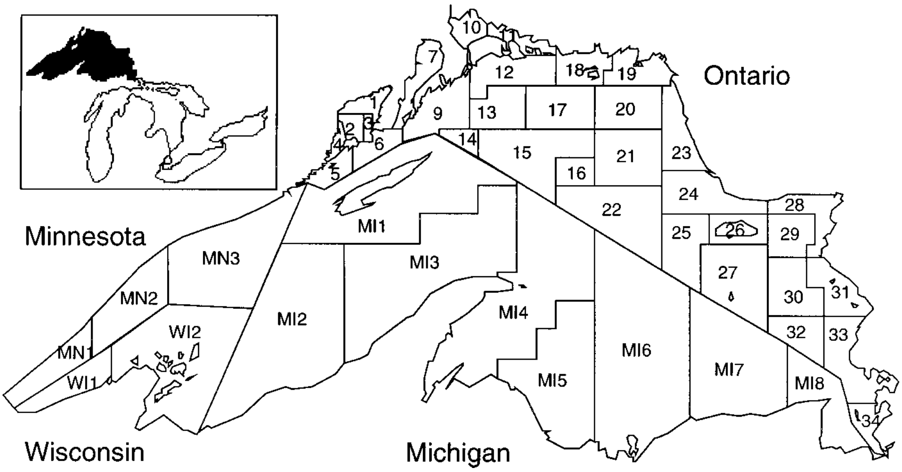

FIGURE 1.—Lake trout management areas of Lake Superior (Hansen et al. 1995b). The letters MI refer to Michigan waters, WI to Wisconsin waters, and MN to Minnesota waters; numbers without letters refer to Ontario waters.

lake trout to be reported in the same field, the morphotype composition was not readily apparent. Therefore, we separated lean and siscowet lake trout catches based on estimated fishing depth and the known depth distribution of these morphotypes. All lake trout catches were coded as siscowet if fishing depths were greater than 65 m and as lean lake trout if fishing depths were less than 65 m. Due to time and budgetary constraints, and because hundreds of commercial fishing licenses were issued historically, the database was developed using information only from large fishing operations (major operators) and from odd-numbered years during the period 1929–1959, as well as 1960 and 1961. We believed that this would maximize the time coverage of data that could be entered under these circumstances. Major operators were defined as fishermen who fished at least 10 times per month and in most months of each year. Major operators accounted for approximately 76% of the large-mesh gill-net effort in Michigan waters of Lake Superior during 1929–1957 (USGS, Great Lakes Science Center, unpublished data).

The annual relative abundance of lake trout from 1959 to 1998 was estimated using assessment gill nets (Pycha and King 1975; Pycha 1980; Hansen et al. 1995a) in eight Michigan management areas (Figure 1). Assessment fishery data included the total number of legal-size (≥432 mm [17 in]) wild and stocked lean lake trout caught, the total weight of the landed catch, fishing effort, gear type (almost all 114-mm, multifilament-nylon gill nets), date, and location (Pycha and King 1975; Hansen et al. 1995a). Wild lake trout were differentiated from hatchery-reared lake trout by the absence of fin clips, as stocked lake trout were marked by the removal of one or more fins according to the year-class. Data were collected every year in management areas MI-3, MI-4, MI-5, and MI-6 from 1959 to 1998 and in MI-7 every year during 1959–1998 except 1992 (Hansen et al. 1995a). Data were collected in MI-8 during 1962–1964, 1966–1982, 1985, and 1996–1998 (Gebhardt 2000). Data were collected in MI-2 during 1970, 1976, and 1986–1998 (Gallinat 1999). Standard 114-mm gill-net data were collected in MI-1 only during 1967, 1979 (Michigan Department of Natural Resources, unpublished data), and 1993, as gill nets with mesh sizes larger than 114 mm were usually used for the assessment in MI-1 (Pycha and King 1975).

Corrections were applied to the historical gill-net data to compensate for the increased efficiency of multifilament-nylon twine, which replaced linen and cotton in the early 1950s (Pycha and King 1975). About 25% of the gill nets fished in 1950 were made of multifilament nylon; in 1951, about 50% of those nets were made of multifilament nylon, and in 1952 nearly all were (Pycha and King 1975). Because multifilament-nylon gill nets are on average about 2.25 times as efficient as linen and cotton gill nets (Hile et al. 1951; Pycha 1962), we multiplied all catches during 1929–1949 by 2.25 and all catches during 1951 by 1.625 (Pycha and King 1975).

Gill-net catches of lake trout vary among mesh sizes (Hansen et al. 1997b) and seasons (Sakagawa 1967). Because the assessment fishery used 114-

mm multifilament-nylon gill nets from late April to early June (Pycha and King 1975; Pycha 1980; Hansen et al. 1995a), we calculated the CPE for commercial fishery lifts using only the catch from 114–120-mm gill nets fished in April–June. To convert the commercial catches from dressed weight to numbers, we divided the weight of the catch by an assumed average dressed weight for a lean lake trout. More specifically, we analyzed our data using three estimates of average dressed weight for lake trout caught in 114-mm gill nets during 1929–1955: 1.09 kg (Rahrer 1967; Lawrie and Rahrer 1972), 1.23 kg (Eschmeyer 1955), and 1.38 kg (Sakagawa and Pycha 1971). The results of the three analyses were qualitatively the same (i.e., the *P*-values were slightly different, but our conclusions were still the same), so we only report the results from the analysis involving the 1.09-kg average weight, which we believe slightly overestimates abundance during 1929–1953 and slightly underestimates it during 1959–1961. We assumed that all of the lake trout caught by the commercial fishery were wild, although lake trout from early stockings may have been present in the late 1950s and early 1960s (Pycha and King 1975). Because gill-net CPE is not a linear function of time, we standardized both the historical and modern values of CPE to a soak time of 1 night using the saturation curve from Hansen et al. (1998).

Data analysis.—We estimated the relative abundance of lean lake trout as the annual unweighted-geometric-mean CPE across all lifts for each management area from 1929 to 1998 (odd years only during 1929–1959). We used geometric means because CPE was lognormally distributed. We also calculated annual CPE for all Michigan waters combined as the unweighted geometric mean of all lifts from 1929 to 1998.

The annual geometric means were used to compare the average relative abundance of lake trout between historical (1929–1943) and modern (1984–1998) reference periods for each management area. The average relative abundance for each reference period was estimated as the unweighted arithmetic mean of the annual geometric means. We used the coefficient of variation (CV = 100 · SD/mean) to compare the variation in abundance in the modern and historical periods (Hansen et al. 1995b).

For each management area, we tested for differences between the average relative abundance in the historic and modern periods with two-tailed Welch's approximate *t*-tests (Zar 1996) because in most areas CPE violated the assumption of equal variance and the sample sizes between periods were not equal. We tested for differences between modern and historic CVs with variance ratio tests of the $\log_e$ transformed geometric-mean CPE for each management area (Zar 1996). We corrected our critical α-value for multiple comparisons with a Bonferroni correction (Neter et al. 1996). Therefore, the critical α-value for our comparisons was 0.0071, which corresponds to 0.05 for a single comparison.

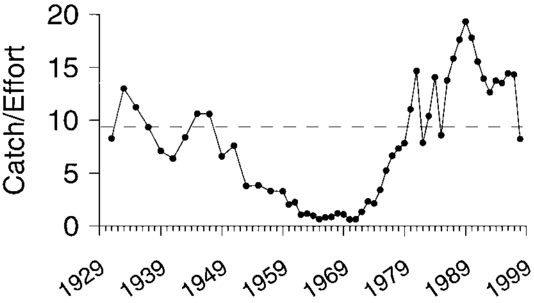

FIGURE 2.—Geometric-mean catch per effort (CPE; number per kilometer of gill net set for 1 night) of wild lean lake trout in all Michigan waters of Lake Superior during 1929–1998. The dashed line shows the average geometric-mean CPE during 1929–1943.

We also examined how fishermen who were targeting lake whitefish may have affected our estimates of lake trout CPE. We recalculated the geometric-mean CPE of lean lake trout for each management area and year after excluding lifts where the catch (by weight) contained more than 50% lake whitefish, more than 25% lake whitefish, more than 10% lake whitefish, or any lake whitefish. We then recalculated the historic mean CPE and compared it with the modern mean CPE to determine whether effort directed at lake whitefish affected our CPE estimates.

Results

In Michigan waters of Lake Superior, lake trout abundance declined from 1929 through the 1960s, increased during the 1970s, and declined during the 1990s (Figure 2). The patterns of change in the relative abundance of lake trout differed somewhat across management areas (Figure 3). In general, the relative abundance of lake trout decreased from 1929 to the 1960s, increased during the 1970s and 1980s, and remained relatively high during the 1990s.

The relative abundance of lake trout (CPE) was generally higher in the modern period (1984–1998) than in the historic period (1929–1943), but

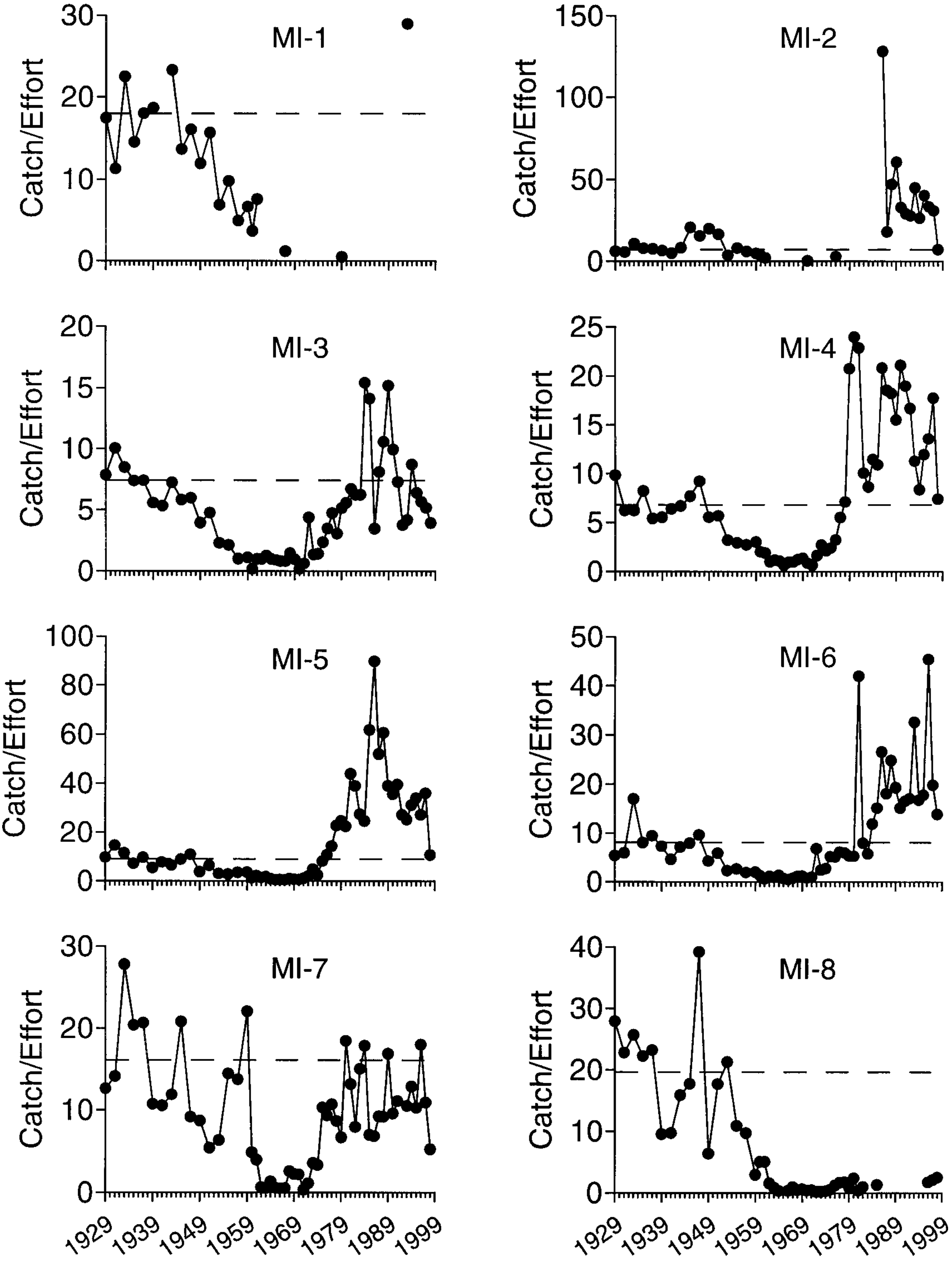

FIGURE 3.—Geometric-mean CPE of wild lean lake trout for eight Michigan management areas during 1929–1998. The dashed lines show the average geometric-mean CPE for each area during 1929–1943.

TABLE 1.—Mean catch per effort (CPE; number per kilometer of gill net set for 1 night) and coefficient of variation (CV = 100·SD/mean) in CPE of wild lean lake trout during historic (1929–1943; commercial fishing data) and modern (1984–1998; assessment fishing data) periods for eight Michigan management areas of Lake Superior. The significance of the differences between historic and modern CPE was determined by Welch's approximate t-test. The significance of the differences between historic and modern CVs was determined by the variance ratio test.

Management area	Historical values		Modern values		CPE comparison			CV comparison		
	CPE	CV	CPE	CV	df	t	P	df	F	P
MI-1	18.0	23.4	29.0[a]							
MI-2	7.2	25.4	40.5	72.9	12	4.05	0.002	12, 7	7.24	0.007
MI-3	7.4	20.5	8.1	51.1	19	0.60	0.557	14, 7	6.10	0.012
MI-4	6.8	21.9	14.8	29.9	18	6.36	<0.001	14, 7	2.65	0.099
MI-5	9.0	33.0	39.7	49.1	15	6.00	<0.001	14, 7	2.39	0.125
MI-6	8.1	48.2	20.7	41.8	20	4.81	<0.001	7, 14	1.34	0.305
MI-7	16.1	38.6	11.1	36.0	10	2.03	0.070	13, 7	1.02	0.517
MI-8	19.6	36.0	1.6	26.2	7	7.06	<0.001	7, 4	2.40	0.208

[a] There was only 1 year of data for MI-1 (1993) during 1984–1998.

the CVs were similar in both periods (Table 1). In MI-2, MI-4, MI-5, and MI-6, the modern abundance was significantly higher than the historic abundance; in MI-3 and MI-7, the historical and modern abundances were not significantly different; and in MI-8 the modern abundance was significantly lower than the historic abundance. The historic relative abundance was highest in MI-8 and lowest in MI-4. The modern relative abundance was highest in MI-2 and lowest in MI-8, though the index of average relative abundance in MI-8 represented only 4 years of data. The relative variation in lake trout abundance (CV) was significantly higher in the modern period in MI-2 but not significantly different in MI-3 through MI-8. The historical abundance was most variable in MI-6 and least variable in MI-3. The modern abundance was most variable in MI-2 and least variable in MI-8.

Indices of wild lean lake trout abundance were similar under all four scenarios of effort targeted at lake whitefish, which demonstrates that our analysis was not sensitive to assumptions about target species. Generally, lifts that contained both lake whitefish and lake trout had a lower CPE of lake trout than lifts that caught exclusively lake trout. However, only 15% of the lifts contained any lake whitefish and not enough lifts contained lake whitefish to make a significant difference in the lake trout CPE.

Discussion

Our indices of historical and modern lean lake trout abundance in the Michigan waters of Lake Superior show patterns (i.e., decreasing abundance through the 1960s and increasing abundance during the 1970s and 1980s) similar to those presented by Hile et al. (1951), Pycha and King (1975), and Hansen et al. (1995b). However, we found that the modern abundance was at least as high as the historic abundance in most areas, which differs greatly from Hansen et al. (1995b), who came to the opposite conclusion. Hansen et al. (1995b) transformed commercial fishery CPE into units similar to those of the assessment fishery using linear relationships during the period when both fisheries were operating (1959–1961). The method used by Hansen et al. (1995b) is valid as long as the conditions that existed in 1959–1961 were constant before that period. However, we believe that Hansen et al.'s (1995b) estimate of historical lake trout CPE was artificially high because the conditions during 1959–1961 were not the same as those during 1929–1943. For example, the average dressed weight of a lake trout caught in the commercial fishery during 1959–1961 was unusually low (0.91 kg; Pycha and King 1975), which inflated their estimate of historical CPE. Also, the average number of nights gill nets were set in 1959–1961 was lower (3.8) than during 1929–1943 (5.1; USGS, Great Lakes Science Center, unpublished data), which also inflated their estimate of historical CPE.

The exclusion of siscowet lake trout lifts from our analysis probably did not greatly affect the results. If we had included them, our conclusions would likely not have changed because commercial fishermen did not start fishing for siscowet lake trout until late June in most years (USGS, Great Lakes Science Center, unpublished data), which is after the spring assessment period we evaluated. Therefore, siscowet lake trout catches would have had little effect on the spring CPE of lean lake trout.

Gear competition, in which setting additional gear lowers the CPE of other gear in the same area (Type III; Ricker 1975), and underreporting of catches may have caused the historic commercial fishery CPE to be an unreliable index of lake trout abundance in Michigan waters of Lake Superior. Gear competition was especially likely in the late 1940s and early 1950s, when fishing effort was extremely high (Pycha and King 1975). Such gear competition could bias lake trout CPE downward in relation to lake trout abundance. In addition, fishermen may have underreported their catches to minimize their federal income tax obligations, which would also reduce CPE. However, our conclusions would not change even if all catches were underreported by 10%, which we believe is unlikely. Consequently, we conclude that gear competition and underreporting of catches did not bias our indices of historical lean lake trout abundance enough to cause it to be greater than the modern abundance.

Management measures to promote and protect naturally reproducing populations have been more successful than previously realized. Even if some of our assumptions are wrong, our sensitivity analyses showed that our conclusions are not greatly affected by them. Therefore, we believe that lean lake trout have been restored to 1929–1943 levels in MI-2 through MI-7. However, the modern abundance of lean lake trout appeared to be lower than the historic abundance in MI-8, possibly because restoration was deferred in this area.

The historic abundance may not be a good goal for lake trout restoration because lake trout stocks may have already been overexploited in many areas of Lake Superior before 1943. Lake trout stocks were locally depleted in Lake Superior as early as the 1880s (Smiley 1882), and yield along the south shore the lake declined during 1900–1924 even though the amount of gear registered remained relatively stable (Koelz 1926). Lawrie and Rahrer (1972) found that lake trout abundance in Michigan waters of Lake Superior decreased about 2% per year from 1929 to 1953. Also, estimates of the historic average dressed weight (1.09–1.38 kg; Eschmeyer 1955; Rahrer 1967; Sakagawa and Pycha 1971; Lawrie and Rahrer 1972) of lean lake trout were smaller than the average dressed weight during 1962–1998 (1.47 kg; Michigan Department of Natural Resources, unpublished data), which may indicate that high fishing mortality rates had truncated the size distribution of lake trout by the early 1930s. The new historical time series we present indicates that lake trout abundance was declining in six of eight management areas during the 1929–1943 reference period and suggests that stocks were already overexploited.

Management Implications

We conclude that self-sustaining populations of lean lake trout have been restored in most Michigan waters of Lake Superior (Hansen et al. 1995a) but that modern stocks may not be able to yield levels of fishery production similar to those in historic times. Lake trout abundance is now at least as high in six of eight Michigan management areas as it was during 1929–1943, when the fishery was thought to be operating near its maximum sustainable yield. Our findings support the decision to discontinue stocking in most Michigan waters of Lake Superior beginning in 1999. However, the Lake Superior community has changed since 1943 (Bronte et al. 1995). The lake trout strains that are present in Lake Superior today are not the same as those before stocks collapsed. Much of the genetic diversity has been lost (Krueger and Ihssen 1995) as historic strains were replaced by a hatchery strain with a lower occurrence of rare alleles than in wild fish (Burnham-Curtis et al. 1995). The food base of lake trout has also changed, as rainbow smelt *Osmerus mordax* are now their predominant prey (Conner et al. 1993) instead of ciscoes *Coregonus* spp. and cottids (Dryer et al. 1965). Sea lampreys are unlikely to be eradicated from Lake Superior and will therefore continue to consume part of the potential lake trout yield.

In most Michigan waters, lake trout abundance is currently higher than during 1929–1943 and will not likely increase dramatically. Using an ecosystem model, Kitchell et al. (2000) found that even the elimination of fishing mortality over a 10-year period did not cause the abundance of lean lake trout to increase substantially in Lake Superior, which suggests that this species may be near carrying capacity. Because conditions in Lake Superior have changed since 1943 and data are not available to assess lake trout abundance before 1929, standards other than CPE are necessary to measure lake trout restoration. One such standard could be the point at which recruitment is reduced through strong density dependence, as indicated by the amount of density dependence in the stock–recruitment relationship in each area (Bronte et al. 1995; Hansen et al. 1997a; Doemel 2000). Analyses that estimate the density dependence of lake trout could provide realistic expectations of lake trout population size and thus benchmarks for restoration.

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