REASSESSMENT OF THE LAKE TROUT POPULATION COLLAPSE IN LAKE MICHIGAN DURING THE 1940s

Great Lakes Fishery Commission

TECHNICAL REPORT 65

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December 2002

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by

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ABSTRACT

Commercial catches of lake trout (*Salvelinus namaycush*) began a steep, unrelenting decline in Lake Michigan in 1944. We assessed whether colonizing sea lampreys (*Petromyzon marinus*), a parasitic fish, or overfishing was mainly responsible for the initial stage of the ensuing lake trout population collapse. Archived records indicate that sea lampreys reached pest levels of abundance by 1946. In northern Michigan waters, catches per unit of effort (CPUEs) of adult lake trout aggregated on six spawning reefs declined between 1942 and 1943. Furthermore, poor recruitment of juvenile lake trout from these same waters, evident in 1949, indicated that lake trout reproduction was impaired as early as 1944. Southern Wisconsin deep reef-spawning aggregations, although possibly diminished by 1947-48, persisted longer than those in northern Michigan waters. The CPUEs (survey) of hatchery-origin lake trout on two reefs in northern Michigan waters were three to five times higher in the 1990s than were CPUEs (commercial) of wild fish during 1929-32. On one deep reef in Wisconsin waters, CPUEs of hatchery lake trout in the late 1990s were seven times higher than those for wild fish in the 1930s and 1940s. Compared to data on the historical commercial fishery, CPUEs of hatchery fish are likely inflated because of reduced genetic diversity and the lack of gear competition in the survey fishery. A marked increase in bycatch of juvenile lake trout during the late 1930s may have contributed to the population collapse of this species in Lake Michigan. Lake trout failed to reproduce in northern waters when spawning populations were still relatively abundant. We suggest that lake trout historically may have controlled the lake's fish community by suppressing potential competitors/predators and that fishing-induced biomass reductions compromised this function.

INTRODUCTION

The invasion of the upper Great Lakes by sea lampreys (*Petromyzon marinus*) in the 1930s and 1940s and the associated collapse of lake trout (*Salvelinus namaycush*) populations were defining biological events for these waters. The sea lamprey likely gained entry first to Lake Ontario via the Erie Canal (passable as early as 1819), and second to Lake Erie as a result of the deepening of the Welland Canal begun in 1913 (Eshenroder and Burnham-Curtis 1999). Once in Lake Erie, sea lampreys had unimpeded access to the upper Great Lakes. Lake trout were the top predator in the upper lakes when sea lampreys invaded (Smith 1968). Lake trout were also the mainstay of the commercial fishery because of the earlier diminishment of lake whitefish (*Coregonus clupeaformis*) populations (International Board of Inquiry for the Great Lakes Fisheries 1943). Although the most-valuable commercial fishes had been declining since the late 1890s (Bogue 2000), invasion by sea lampreys combined with the loss of lake trout led to substantial recovery efforts (Holey et al. 1995). A rich literature subsequently evolved where, surprisingly, the role of the sea lamprey in the lake trout population collapse is still controversial.

Among the three upper Great Lakes, the controversy regarding the role of the sea lamprey in precipitating population collapses of lake trout centers on Lakes Michigan and Huron. No author has disputed the analysis of Hile et al. (1951) showing that lake trout catches per unit effort (CPUEs) in Lake Superior were trending downward well before sea lampreys could have been a contributing factor. In their re-analysis of the data on Lake Huron, Coble et al. (1990) concurred with Hile (1949) that the sea lamprey and not overfishing was the cause of the collapse in this lake. However, the analysis was challenged by Eshenroder (1992), Eshenroder et al. (1995b), and Hansen (1999). Hansen (1999) also questioned Coble et al. (1990) on their interpretation of the data on Lake Michigan. Coble et al. (1990) had concurred with Hile et al. (1951) and Eschmeyer (1955) who both reported that sea lampreys were responsible for the lake trout population collapse in Lake Michigan. Sea lampreys were first observed in Lake Michigan in 1936 and landings of lake trout began a steep, unrelenting decline in 1944 (Fig. 1).

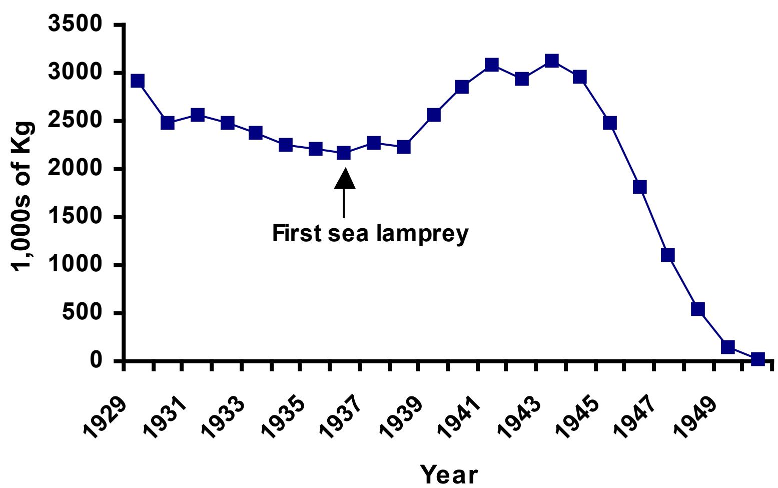

Fig. 1. Commercial landings of lake trout from Lake Michigan, 1929-1950.

The controversy still exists as to whether the cause of the decline of lake trout in Lake Michigan was sea lampreys or overfishing. If lake trout populations were in serious decline before sea lampreys became abundant, overfishing would be the apparent cause—at least in the early stages of the collapse. The reverse would be true if lake trout populations were not in decline. It is important to note that none of the studies of Lake Michigan lake trout used all of the available information about when:

- Sea lampreys became abundant

- Lake trout recruitment began to fail

Moreover, Eschmeyer (1955), who undertook the most-detailed analysis of the Lake Michigan collapse, was at a disadvantage because the biology of sea lamprey parasitism on lake trout was not well understood. For example, investigators at the time were not sure whether sea lampreys preferred juvenile or adult-sized lake trout as prey, which led to problems in deciphering a signal of sea lamprey impacts. Furthermore, early investigators working on the sea lamprey problem had anticipated, based on research in Lake Ontario, the ensuing collapse of the lake trout population in the upper lakes (Eshenroder 1992). A foregone conclusion that sea lampreys would be responsible for the soon-to-follow losses of lake trout was understandably hard to resist. Scientists at the time tended not to be as objective in examining the alternative hypothesis as they might have been. Furthermore, because of the scientists' professional stature, they may have unduly influenced subsequent investigators.

Despite an extensive history of publication, the sea lamprey vs. overfishing controversy remains fruitful for further exploration. The Lake Michigan case is particularly interesting because this lake produced more lake trout (Eshenroder et al. 1995a) and contained more lake trout spawning habitat (Dawson et al. 1997) than any of the other Great Lakes. These features suggest that the lake trout population in Lake Michigan should have been more resilient to commercial fishing than populations in the other upper lakes, thus favoring the sea lamprey hypothesis. Also noteworthy, and unlike the other upper lakes, commercial daily catch reports—including effort and fishing locations—are available for nearly all of Lake Michigan for the period when the lake trout collapse was under way. These ingredients combined with a more-prolific lake trout population and richer data make a more-thorough analysis of the lake trout population collapse in Lake Michigan attractive. Eshenroder (1992) suggested that commercial catch statistics should be disaggregated in further studies to better account for population heterogeneity. This approach remained to be undertaken until now even though it had additional prospects for providing insights into the current, unsuccessful efforts to reestablish self-reproducing populations of this species in Lake Michigan (Holey et al. 1995). Dawson et al. (1997) had quantified differences in spawning-aggregation CPUEs among sites in Lake Michigan during the 1930s. Here we use their approach to examine CPUEs for the most-prominent spawning aggregations during the 1940s when the population collapse was occurring.

Our primary objectives in this study of sea lampreys and lake trout in Lake Michigan were to:

- Identify more precisely when sea lampreys reached pest levels of abundance

- Determine when recruitment of lake trout began to fail in three separate regions of the lake

Our secondary objective was to compare historical CPUEs for wild lake trout with contemporary CPUEs for stocked lake trout, which should be helpful in benchmarking current efforts to build spawning populations.

METHODS

Sea Lamprey Colonization

We searched for data regarding sea lamprey population increases in Lake Michigan during the 1940s in the reports and proceedings of several committees that met during this decade—the proceedings of the 1946 Sea Lamprey Conference and minutes of the Great Lakes Sea Lamprey and Lake Trout committees, whose genesis has been described by Smith and Tibbles (1980). We also looked for relevant comments made by commercial fishermen in their "Daily Reports of Commercial Fisheries of the Great Lakes." These reports were submitted monthly and provided an efficient method for fishermen to communicate with fishery officials.

Historical Lake Trout Populations

To establish when lake trout populations declined in Lake Michigan, we reconstructed CPUEs (kg of trout/304 m of net lifted) for lake trout gillnetted commercially on spawning reefs during October and November, the presumptive spawning period. The information (operator, date, location, effort, and catch of lake trout and whitefish) taken from daily catch reports was entered into a database following Dawson et al. (1997). We focused on clusters of spawning reefs that were the largest producers in three regions: northern Michigan and Wisconsin waters, and southern Wisconsin waters (Fig. 2) (Dawson et al. 1997):

- Six reefs were selected from northern Michigan waters: Big Reef, Dahlia Shoal, Fisherman's Island, Fox Islands (North and South), Gull Island (including Gull Island Shoal), and Point aux Barques

- In northern Wisconsin waters, where effort on spawning reefs was relatively low, CPUEs were entered for only three reefs: Cardys Reef, Port of Baileys Harbor (various small reefs were fished from this port), and Whaleback Shoal

- All four of the deep reefs in southern Wisconsin waters were analyzed: East Reef, Milwaukee Reef, Northeast Reef, and Sheboygan Reef

In each region, data entry started in a year when the decline in annual (all months) CPUEs for gillnets was well under way. From this apparent midpoint of the population collapse, we worked back in time until spawning-season CPUEs peaked (pre-collapse years) and ahead in time until the number of lifts was so low that statistical analysis was clearly precluded, because the population collapse was essentially complete.

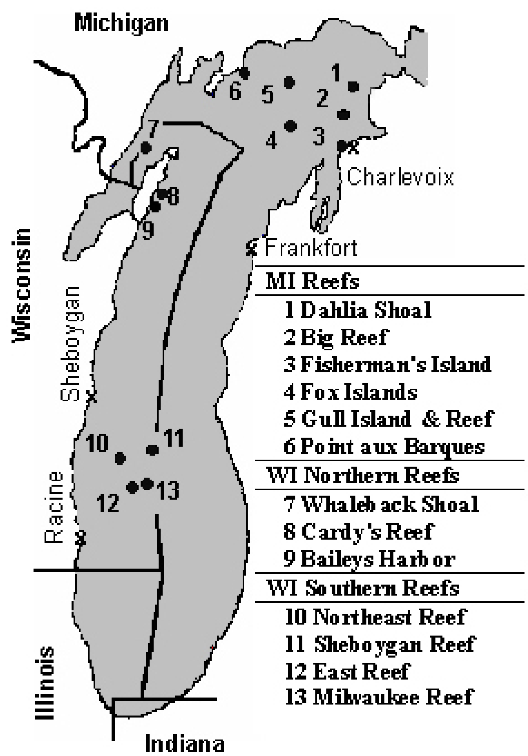

Fig. 2. Locations of lake trout spawning reefs and ports referred to in this study.

Our analysis was constrained by seasonal fishing closures aimed at protecting spawning lake trout. Dawson et al. (1997) could analyze the state of Michigan catch data for most of October and all of November in 1929-32 because an extensive fishery operated under permits to collect spawn for hatcheries during the closed season. The permit fishery in Michigan ended after 1932 leaving for the 1940s (the period of interest to us) only those lifts made during the open season—October 1-10 and November 11-30. We focused on the later period, November 11-30, for two reasons (Dawson et al. 1997):

- Spawn collection for a federal hatchery in the state of Michigan showed that spawning fish were still plentiful when the season reopened on November 11

- Spawning fish were not fully aggregated on the reefs before October 11

Although the permit fishery in the state of Wisconsin waters continued after 1934-37 (the years studied by Dawson et al. (1997)), the number of permits issued was reduced in the early 1940s, and the program ended after 1945. Cutbacks in the permit fishery severely limited the number of lifts made in northern Wisconsin waters where fishing on spawning reefs was already light. We used the northern Wisconsin data for October and November during the 1940s to establish only the pattern of dwindling effort—an indication of fish abundance. The southern Wisconsin spawning-aggregation fishery was much larger than that in northern waters. However, the complete closure of the permit fishery after 1945 required focusing exclusively on lifts made after November 16 when the closed season ended.

We examined how well late-spawning-season CPUEs tracked whole-spawning-season CPUEs. For our six study reefs in Michigan waters, we compared late-season (November 11-30) CPUEs and whole-season CPUEs for 1929-32 when harvest occurred during the whole season (data from Dawson et al. (1997) available at http://www.glfc.org/databases/michigan.asp). An Analysis of Variance (ANOVA) with year and location (reef) as effects was used to estimate mean CPUEs and standard errors by year. These data, however, were unbalanced because two of our six northern Michigan reefs were not fished during the late season in 1932. To accommodate the partial data, we conducted four ANOVAs:

- Two using four reefs only (Big Reef, Fisherman's Island, Gull Island, Point aux Barques) for all four years

- Two using all reefs for three years (1929-31)

We visually compared the means and standard errors estimated by each ANOVA to assess how well late-season CPUEs tracked CPUEs that were better centered on the spawning season.

We used data from 1943-45 instead of data from 1934-37 (Dawson et al. 1997) to determine how well late-season CPUEs (November 17-30) tracked whole-season CPUEs (30 October to 30 November) for the four southern Wisconsin reefs. Severe restrictions on permit fishing during 1943-45 apparently encouraged increased fishing effort in late November making the 1943-45 data more insightful for our analysis. The 1943-45 data, however, were also unbalanced, necessitating, as before, four ANOVAs:

- East and Milwaukee reefs for all three years (whole-season and late-season CPUEs)

- All four reefs for 1944 and 1945 (whole-season and late-season CPUEs)

We again used ANOVA to calculate mean CPUEs and standard errors.

For regions where late-season CPUEs tracked whole-season CPUEs, we tested for year-to-year differences in CPUEs using ANOVA with year, reef, and year x reef as categorical effects. This test incorporated all available late-season CPUEs—our 1940s data and data from Dawson et al. (1997), which encompassed 1929-32 for Michigan waters and 1934-37 for Wisconsin waters. Including data from Dawson et al. (1997) ,allowed us to see how the pre-collapse (higher) CPUEs from the 1940s compared with CPUEs from an earlier time when the fishery was regarded as healthy. Following the ANOVA, Tukey's pairwise comparisons were used to detect significant ($\alpha = 0.05$) declines in CPUEs between adjacent years.

Contemporary Lake Trout Populations

Survey CPUEs for contemporary (hatchery-origin) populations of spawning lake trout were available for three of the reefs in our 1940s data set:

- Fisherman's Island
- Gull Island Reef and Shoal
- Sheboygan Reef

The CPUEs for the lifts made on Gull Island were provided by the senior author of Madenjian and DeSorcie (1999). Data on six lifts of large-mesh gillnets made on Fisherman's Island in the last half of October from 1996 to 1999 were also located (R. Claramunt, Little Traverse Bay Band of Odawa Indians, P.O. Box 246, Petoskey, MI 49770 and J.L Jonas, Michigan Department of Natural Resources, Charlevoix Fisheries Station, 96 Grant St., Charlevoix, MI 49720, personal communications). Sheboygan Reef was assessed with large-mesh gillnets from 1983 to 1999 with most lifts clustered from October 27 to November 5 (P. McKee, Wisconsin Department of Natural Resources, 110 S. Neenah Avenue, Sturgeon Bay, WI 54325, personal communication). Contemporary CPUEs were converted from numbers of fish to kilograms of fish (not necessary for Gull Island): 3.60 kg/fish for Fisherman's Island and 3.30 kg/fish for Sheboygan Reef (Madenjian and DeSorcie 1999). Catch for contemporary lifts was decreased by a factor of 2.25 to account for the increased efficiency of the nylon multifilament gillnets (Pycha 1962) used in these surveys.

The historical data in our comparisons of historical and contemporary CPUEs include data from Dawson et al. (1997) and CPUEs from the 1940s. The Dawson et al. (1997) data from all of October and November are better centered on peak spawning than are our late-season CPUEs from the 1940s. To help offset this bias, we used all available data for lifts made in October and November during the 1940s. This convention allows the inclusion of the October CPUEs for days before the spawning closure and the limited number of permit-fishery CPUEs from southern Wisconsin waters. Thus, the CPUEs in our comparison of contemporary and historical CPUEs and those used to assess the population collapse of the 1940s are based on different days.

To smooth our comparisons of historical and contemporary mean CPUEs, we combined CPUEs for adjoining years. Intervals of four years (one exception of five years) for Michigan reefs and intervals of two to four years (mostly three years) for Sheboygan Reef were selected to compensate for discontinuities in the data sets. Mean and 95% confidence intervals were calculated for each group of years.

Data Treatment

All statistical tests were done with SYSTAT v. 9.0. The CPUEs were transformed to $\log_e$ (CPUE + 1) for analysis to approximate a normal distribution. Non-logarithmic data in figures have been back-transformed using the method of Hayes et al. (1995).

RESULTS

Sea Lamprey Colonization

The earliest quantitative or qualitative data on sea lamprey marking rates for lake trout in Lake Michigan were from 1947. Of 902 lake trout landed at Wisconsin ports (Racine to Sheboygan, Fig. 2), 45% had one or more marks according to the minutes of the 1947 Great Lakes Sea Lamprey Committee. Insomuch as these fish were taken from March 3 to April 2, the marks reflect attacks made by sea lampreys that had reached the late juvenile stage in the fall of 1946. A Wisconsin commercial fisherman reported "a definite increase in the number of fish [lake trout] attacked" and marking-rate estimates (not actual counts) of 50%-75% in the minutes of the 1946 Great Lakes Sea Lamprey Conference. Subsequent committee reports indicate that marking rates remained high after 1946. We found only one notation on a daily catch report relating to sea lampreys. A fisherman collecting lake trout spawn in northern Michigan waters in 1946 wrote "the eels (sea lampreys) were sure after the trout this fall."

Historical Lake Trout Populations

For our six study reefs in northern Michigan waters, late-season CPUEs closely tracked whole-spawning-season CPUEs in both comparisons (Fig. 3):

- All six reefs for three years (1929-31)

- Four reefs (Fisherman's Island, Gull Island, Big Reef, and Point aux Barques) for four years (1929-32)

This finding cleared the way for us to test for year-to-year changes in CPUE. Categorical effects (year, reef, year x reef) explained 35% of the variation in CPUE (P <0.001). Mean CPUEs in adjacent years did not decline from 1929 to 1942 (no data for 1932-39) (Fig. 4). The first significant decline in CPUE occurred in 1943 (P = 0.01) and a second, more-pronounced decline occurred in 1947 (P < 0.001).

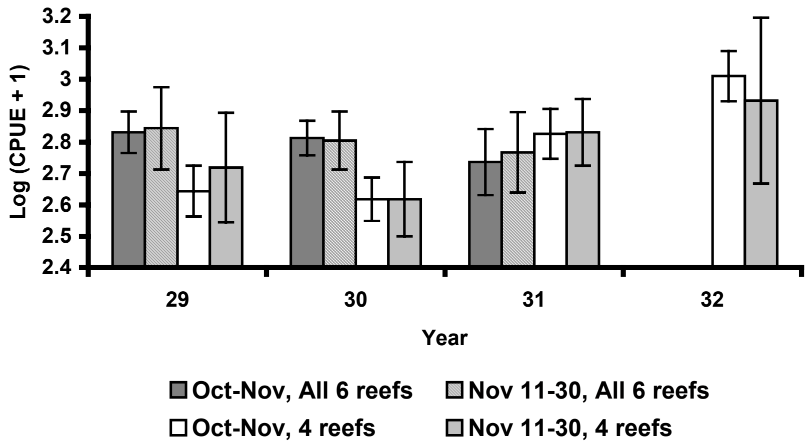

Fig. 3. Two comparisons of whole-season mean CPUEs (October-November) and late-season mean CPUEs (November 11-30) for spawning lake trout in Lake Michigan: six northern Michigan reefs combined, 1929-31 and a subset of four of the reefs combined, 1929-32.

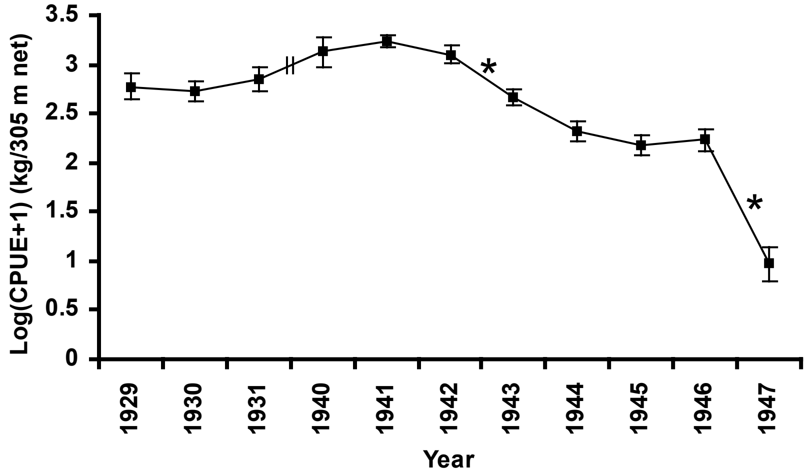

Fig. 4. Mean CPUEs (November 11-30) for lake trout on six spawning reefs in northern Lake Michigan, 1929-47 (no data for 1932-39). Asterisks denote a significant pairwise difference. Error bars are ± one standard error.

Late-season CPUEs (November 17-30) did not track whole-season CPUEs (30 October-30 November) on the southern Wisconsin deep reefs in either of two comparisons using 1943-45 data (Fig. 5). The relationships were distorted by high late-season CPUEs in 1944. Because of this lack of pattern, we did not test for significant declines in CPUEs for adjacent years. Fishing effort (number of lifts) during the late season was remarkably light—only 12 lifts from 1934 to 1937 as compared to 1942-46, when 310 lifts were made (Fig. 6). Effort on the deep reefs dwindled away in 1947 and 1948. The CPUEs were also lower in 1934-37 than in the early 1940s.

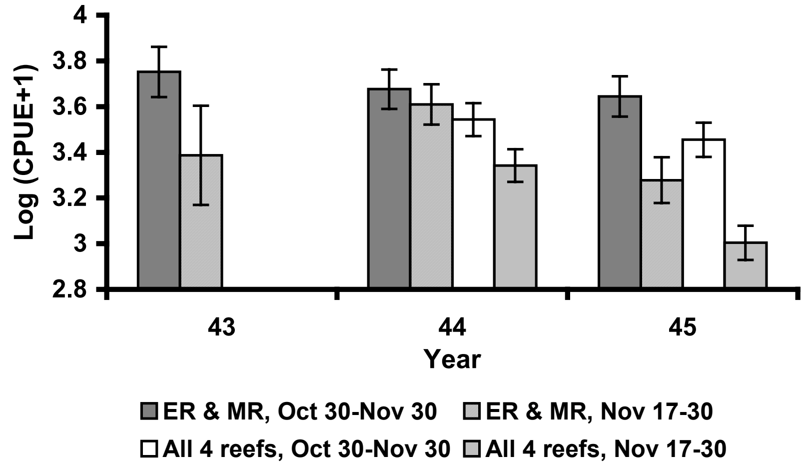

Fig. 5. Two comparisons of whole-season mean CPUEs (October 30-November 30) and late-season mean CPUEs (November 17-30) for lake trout on deep spawning reefs in southern Lake Michigan: East Reef (ER) and Milwaukee Reef (MR), 1943-145, and all four reefs: ER, MR, Northeast Reef, and Sheboygan Reef, 1944-45. Error bars are ± one standard error.

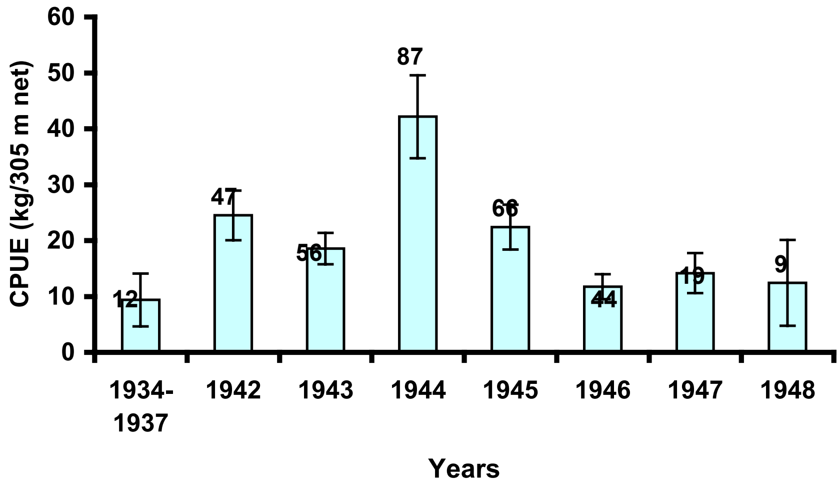

Fig. 6. Mean CPUEs (November 17-30) for lake trout on all four deep reefs in southern Lake Michigan, 1934-37 (combined) and 1942-48 (individual years). The number at the top of a bar is the number of lifts. Error bars are 95% confidence intervals.

On the northern Wisconsin reefs, fishing effort was higher in 1935-37 than in the early 1940s (Fig. 7)—the reverse of the pattern seen on the southern deep reefs. Fishing effort ceased on the northern Wisconsin reefs in 1946—a year earlier than on the southern deep reefs.

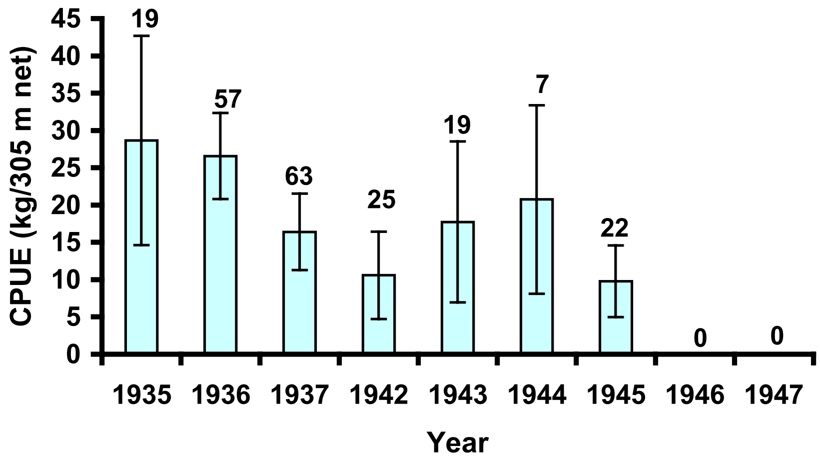

Fig 7. Mean CPUEs (November 17-30) for lake trout on three spawning reefs in northern Wisconsin waters of Lake Michigan, 1935-47 (no data for 1938-41). The number at the top of a bar is the number of lifts. Error bars are 95% confidence intervals.

Contemporary Lake Trout Populations

Whole-season CPUEs on Fisherman's Island and Gull Island (northern Michigan reefs) were 3-5 times higher for the hatchery-origin population of the 1990s than for the wild populations of 1929-32, the early 1940s, or the mid-1940s (Fig. 8). A similar pattern was evident for Sheboygan Reef (Fig. 9), which also includes CPUEs for hatchery-origin fish throughout the 1980s. The CPUEs for hatchery lake trout on Sheboygan Reef in the 1980s through the early 1990s were comparable to historical CPUEs. Abundance of hatchery lake trout increased dramatically later in the 1990s in response to increased stocking. By 1998-99, stocked lake trout were sevenfold more plentiful on Sheboygan Reef than were wild fish in the 1930s or 1940s.

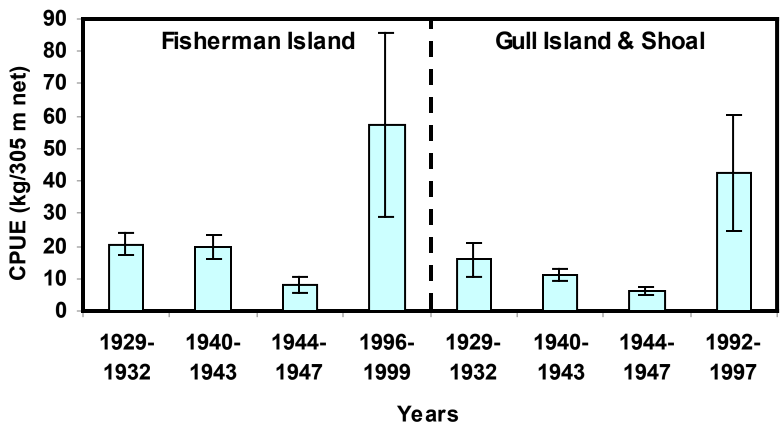

Fig. 8. Mean CPUEs for wild (1929 through 1947) and hatchery-origin (1990s data) lake trout on Fisherman's Island and Gull Island (includes Gull Island Shoal) in northern Lake Michigan from October 1 to November 30. Error bars are 95% confidence intervals.

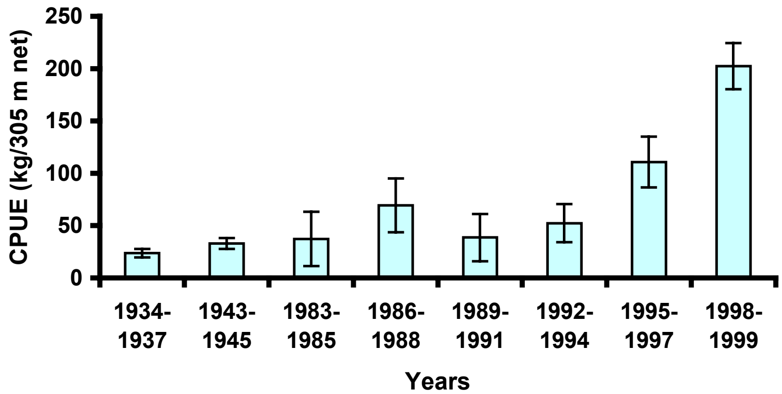

Fig. 9. Mean CPUEs for wild (1934 through 1945) and hatchery-origin (1980s and 1990s) lake trout on Sheboygan Reef from October 1 to November 30. Error bars are 95% confidence intervals.

DISCUSSION

Sea Lamprey Colonization

Historical information on sea lamprey abundance in Lake Michigan indicated that they were at a destructive level by 1946 in the northern half of the lake. Marking rates on lake trout in that year (45% were marked) were higher than in 1950 in South Bay, Lake Huron, where marking rates on the largest lake trout varied from 20%-30% and natural mortality was estimated at 70% (Fry 1952). Smith (1968), however, proposed that sea lampreys were not abundant in Lake Michigan until the early 1950s. His argument, which was restated by Hansen (1999), is based on the number of sea lampreys spawning in Hibbards Creek, a tributary in the northwest region of the lake. This spawning run—the first from the lake to be enumerated by weir—was small from 1946 (the first year of operation) until 1950. Smith (1968) further noted that the spawning runs in Hibbards Creek during 1955-59 correlated with the combined runs in three other rivers first sampled in 1955. He hypothesized that had these three streams been sampled as early as 1946, they too would have had small runs similar to those seen in Hibbards Creek in the late 1940s. In hindsight, Hibbards Creek was probably a poor choice for the location of the first weir on Lake Michigan. It is a marginally productive stream for sea lampreys (D. Lavis, United States Fish and Wildlife Service, 229 S. Jebavy Dr., Ludington, MI 49431, personal communication) and likely was not very attractive to the colonizing population. As indicated by the 1946 marking data, strong spawning runs of sea lampreys must have occurred at least in northern streams by 1947.

We argue that sea lampreys could not have reached pest levels of abundance before 1946 even though we could not locate any quantitative data on their pre-1946 abundance. Eshenroder (1992) hypothesized that sea lampreys would have needed two generations, at least ten years, to reach pest levels, given the small founding population. Researching Lake Huron, he showed that 10 years elapsed between colonization and recognition by fishermen that sea lampreys were at pest levels of abundance. He also showed that depending on what year, 1938 or 1946, is taken as the entry date for sea lampreys in Lake Superior, a minimum of either 18 or 10 years, respectively, were required to reach a population level judged to be incompatible with lake trout rehabilitation. Coble et al. (1990) countered that the founding population, in this case for Lake Huron, could have been in the thousands, thus eliminating one generation. Founding by mass migration seems unlikely for Lake Michigan. These lampreys would have had to come from Lake Huron where the first sea lamprey was not seen until 1937. The two-generation hypothesis is consistent with events in Lake Michigan—colonization in 1936 and pest levels of abundance in 1946. If sea lampreys achieved pest levels of abundance before 1946, which we doubt, a small number of founders would have had to have been much more prolific than they were in Lakes Huron and Superior.

Historical Lake Trout Populations

Our analysis indicates that, in northern Michigan waters, the abundance (as CPUE) of spawning lake trout declined significantly in 1943 (Fig. 3), two years before any evidence of a decline in lakewide landings (Fig. 1, see also Hile et al. 1951). The decline in abundance of spawning lake trout between 1946 and 1947, however, was even more severe and signaled the end of this fishery. Why did this significant decline not occur a year earlier, in 1946, the year we identified as the first year that sea lampreys reached pest levels of abundance in northern waters? One explanation involves the growth of juvenile (parasitic stage) sea lampreys. Juvenile size increases abruptly in October and November in the Great Lakes (Swink 1990; Bergstedt and Swink 1995), making attacks on large fish, such as mature lake trout, especially lethal (Schneider et al. 1996). Our CPUEs for northern Michigan waters reflect abundance November 11-30 and are biased toward the first days of this period when fishermen were anxious to set nets before spawning ended. Consequently, our estimate of abundance for 1946 does not reflect the full impact that sea lampreys made on spawning-size lake trout in that year.

Fishing effort on northern Wisconsin spawning reefs ceased in 1946 (Fig. 7), indicating that these populations collapsed a year earlier than those in northern Michigan waters. Spawning aggregations in northern Wisconsin waters were much smaller than those in northern Michigan waters (Dawson et al. 1997), making a less favorable (for lake trout) predator-to-prey ratio in this region. Fishing regulations, also, were changing at the time. In 1946, for the first time, fishing was limited exclusively to the open season because the Wisconsin hatcheries had closed the year before. Despite this restriction, we believe that the abandonment of fishing for spawning lake trout in 1946 reflected a scarcity of fish. From 1942 to 1945, when permit fishing was constrained, open-season effort on the three spawning reefs that we studied averaged ten lifts per year. The gillnet fishery still existed in 1946 and would seemingly have been located on these spawning reefs had fish been available.

Lake trout spawning aggregations persisted longer (through 1948) on the southern Wisconsin deep reefs than in northern Michigan waters, according to our CPUE data (Fig. 6) and Eschmeyer (1955). Our effort data, however, suggest that fishing opportunities on the deep reefs were diminishing as early as 1947. Our Wisconsin CPUE data are somewhat problematical because spawning was nearly over by the time the season opened on November 17, seven days later than in Michigan waters. We believe these factors make the CPUE estimates more vulnerable to variations in how long spawning lake trout stayed on the reefs. Despite these caveats, the deep-reef fishery, although possibly impaired by 1947-48, clearly persisted longer than the northern Michigan spawning-aggregation fishery.

The low CPUE and effort on the southern Wisconsin deep reefs in 1934-37 compared with the 1940s (Fig. 6) is a curiosity. One might expect that spawning lake trout would have been more abundant earlier at this important location because the lake trout fishery had been gradually diminishing since the turn of the century (Wells and McClain 1973). We suspect that the explanation lies in the fact that, in the 1930s, the permit fishery was flourishing. In that era, by the time the season reopened on November 17, the spawning populations had already been fished heavily. We did not, however, see a pronounced upward bump in CPUEs in northern Michigan waters in the 1940s (Fig. 3) even though the permit fishery there ended after 1932. The CPUEs rose slightly in the early 1940s but not enough to be detected in our pairwise comparison of adjacent years.

Contemporary Lake Trout Populations

On the three reefs where we could make comparisons, CPUEs of hatchery-origin lake trout during the 1990s were markedly higher than CPUEs of native fish (Figs. 8, 9). Disparities in gear competition and genetic composition between the historical and contemporary periods tend to inflate the CPUEs of hatchery fish. The historical fishery was competitive, whereas the present-day survey fishery is not. Had only one operator fished the historical spawning runs, historical CPUEs would surely have been more comparable to those of the 1990s. We have no way of correcting for differences in gear competition.

Although numerous strains of lake trout have been used for egg collections since the wide-scale stocking of Lake Michigan began in 1965, none of the strains has undergone selection in Lake Michigan for generations. Could non-native lake trout be more clustered on some reefs and more vulnerable to netting than native fish? We have one insight here. Various sites on Sheboygan Reef were explored as potential locations for assessment fishing but only one produced the desired numbers of fish. It became the reference site (M. Holey, United States Fish and Wildlife Service, 1015 Challenger Ct., Green Bay, WI 54311, personal communication). We seriously doubt that the native population was this clustered. Competition would likely have favored selection for a native spawning population that dispersed over large structures such as Sheboygan Reef (Coberly and Horrall 1980). One of the strains stocked on Sheboygan Reef is a hybridized native (Holey et al. 1995; Eshenroder et al. 1999) but much of the diversity of the native populations has been lost (Brown et al. 1981). This loss of diversity would, we believe, result in reduced use of spawning habitat and, more importantly, inflated CPUEs.

When Did Lake Trout Reproduction Fail?

Our data for the northern waters of Lake Michigan indicate that the abundance of spawning lake trout dropped significantly in 1943, three years before sea lampreys likely reached pest levels of abundance. Was this decline a signal of reduced reproduction or an unexplained, relatively benign event? A heretofore-overlooked study (Van Oosten 1950), published in a commercial-fishing trade journal by the then-chairman of the Great Lakes Lake Trout Committee, bears on this question.

Under the aegis of the Lake Trout Committee, 3.3-million lake trout fingerlings were stocked near Charlevoix, Michigan, during 1944-46. Some 12.6% of these fish were marked by fin clip, and an extensive effort was made to recover juveniles taken as bycatch in the fishery for deepwater ciscoes (marketed as chubs, *Coregonus* spp.). This study emphasized dispersal and absolute return of the clipped lake trout rather than ratios of hatchery to wild fish. We could locate only one record that gave the percentage of recovered fish that were clipped even though 1,000 juveniles, with what were considered bona fide clips, were collected during 1947-1949. Inspections near Charlevoix in May of 1949 resulted in the recovery of 105 juvenile lake trout of which 14 (13.3%) were clipped.

Insomuch as the ratios for clipped and recovered, clipped lake trout are nearly identical. The unclipped lake trout in the May 1949 sample should also have been mostly of hatchery origin, implying that wild juveniles were already scarce in 1949. Alternative explanations (for example, that hatchery-origin and wild juveniles occupied different habitats or that the number of lake trout stocked was large in relation to typical levels of wild recruitment) are less plausible (Eck and Brown 1985). The stocked fish originated from egg collections in northern Michigan waters, were reared in the Charlevoix hatchery and were planted on nearby Big Reef, which had supported the largest spawning aggregations in the northern half of the lake (Dawson et al. 1997). The scarcity of wild fish in the Charlevoix area extended southward at least to Frankfort. Eschmeyer (1955) reported that wild juveniles taken by Frankfort fishermen in 1949 were only 7% as abundant as they were in 1930-31. Therefore, the depletion of juvenile lake trout by 1949 was not a local phenomenon—it extended over a large area of northeastern Lake Michigan, which included the largest aggregation of spawning habitat in the lake (Dawson et al. 1997).

Reproduction of lake trout would have had to fail at least by 1944 to account for a scarcity of wild juveniles in 1949. Age-4 was the dominant age group in the May 1949 sample (Van Oosten 1950) as it was for wild lake trout caught in experimental chub nets fished in Lake Michigan during 1930-32 (Van Oosten and Eschmeyer 1956). A reproductive failure as early as 1944 is consistent with our detection of the first significant decline in CPUEs of spawning lake trout in northern Michigan waters in 1943.

Pinpointing the year when reproduction failed elsewhere in the lake is more difficult. At some point, sea lampreys likely switched to feeding on smaller prey, including juvenile lake trout. Such losses could erroneously be interpreted as reproductive failure. Juvenile lake trout of the size taken in chub nets, however, were partially sheltered from sea lampreys by other species of fish, including chubs. Insomuch as twice as many clipped juvenile lake trout were recovered in 1949 as in 1948 (even fewer were taken in 1947), we suggest that Eschmeyer's (1955) low bycatch estimates for southern Michigan waters in 1950 reflect reproductive failure rather than direct losses attributable to sea lampreys. Bycatch in these waters then was only 4% of what it was in 1930-32 suggesting that the reproductive source for these waters gave out as early as 1945. Reproduction can also be inferred to have ended when spawn collections failed. Spawn collections were marginal in northern Michigan waters in 1946 and gave out in 1947. In Illinois waters, substantial amounts of spawn (380 kg) were last collected in 1947 according to the 1947 report of the Great Lakes Lake Trout Committee. The complete failure of spawn collection, we caution, provides only the latest date that reproduction could have been successful. In northern Michigan waters, reproduction apparently failed three years before spawn collections failed.

CONCLUSIONS AND SPECULATIONS

A major objective of this paper was to narrow the windows during which sea lampreys became abundant in Lake Michigan and lake trout recruitment failed. The window when sea lampreys reached pest levels of abundance had extended from 1945 (Coble et al. 1990) to 1950 (Smith 1968). The historical evidence that we present shows that sea lampreys were destructive by 1946—a date in line with Coble et al. (1990). The window for lake trout recruitment failure extended from 1945 or 1946 (Smith 1968) to the early 1950s (Eschmeyer 1955). Our analysis indicates that the abundance of spawning lake trout declined in northern Michigan waters, an area rich with spawning reefs in 1943, and that reproduction failed at least by 1944, dates that are more supportive of Smith (1968). Our analyses for other regions of the lake are less clear. Spawning populations in northern Wisconsin waters ended completely in 1946, too early to assign culpability entirely to sea lampreys. The source of recruits for southern Michigan waters was depleted by at least 1945. The whereabouts of this source of recruits is unknown—there were no spawning reefs in these waters (Dawson et al. 1997). This mystery makes an association between lake trout recruitment in southern Michigan waters (Eschmeyer 1955) and changes in abundance of specific spawning aggregations tenuous.

Wells and McClain (1973) believed that adult lake trout populations were excessively fished in Lake Michigan well before sea lampreys reached pest levels of abundance. Arriving when they did, sea lampreys could have obscured what was then decipherable had the biologists of the time realized either that sea lampreys much prefer adult over juvenile lake trout as prey or that the results of their stocking experiment were alarming. Eschmeyer's (1955) paper should have alerted later authors that lake trout reproduction was failing as early as 1944-45. Unfortunately, the ramifications of Eschmeyer's data showing that the abundance of juvenile lake trout was declining more rapidly than the abundance of large lake trout were overlooked.

The chub fishery may have precipitated the population collapse of lake trout. Eschmeyer (1955) showed that bycatch of lake trout in the chub fishery at times exceeded the number of lake trout taken in the target fishery. However, Eschmeyer did not think that such losses were implicated in the population collapse. He surmised that an especially intensive bout of chub fishing in 1935-38 was benign because landings of lake trout were strong in 1939-44. We show, however, that reproduction was failing at least by 1944. Therefore, the increase in chub fishing in Lake Michigan does correlate with the lake trout reproductive failure.

We believe that a spate of intensified fishing for juvenile lake trout with an intensive fishery already targeted at adults left too few spawning-sized fish in the population. Spawning aggregations of lake trout in northern Michigan waters were abundant enough in 1944 and 1945 to supply the Charlevoix hatchery, despite the closed season, but were not able to reproduce successfully themselves. This situation mirrors what Walters and Kitchell (2001) call cultivation/depensation, a process where large-bodied fish species control the abundance of small-bodied competitors/predators of their own juveniles. Lake trout, because it is the only entirely freshwater fish occurring in high latitudes in North America (Lindsey 1964), is viewed as an early colonizer following retreating glacial margins (Wilson and Hebert 1996). The species likely dominated Lake Michigan for thousands of years, suppressing populations of ciscoes and sculpins (*Cottidae* spp.), thus protecting its own juveniles from the full effects of predation/competition by these species. The lake trout population may not have been able to compensate for the increased removal of juveniles in the 1930s. By the early 1940s, egg deposition would have been declining at the same time that prey species were being released from predation, thus accounting for year-class failure at least by 1944.

Stocked lake trout are not likely plentiful enough to achieve dominance (Eck and Brown 1985). Although the CPUEs that we present for stocked lake trout on three reefs look impressive, most of the reefs used historically support low numbers of stocked lake trout. For example, Big Reef and Dahlia Shoal, which supported the largest spawning aggregations in northern waters, are nearly devoid of stocked lake trout (J.L Jonas, Michigan Department of Natural Resources, Charlevoix Fisheries Station, 96 Grant St., Charlevoix, MI 49720, personal communications). The message from the past is that, if rehabilitation of lake trout in Lake Michigan is to be successful, it will require a population of hatchery fish large enough to achieve ecological dominance.

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