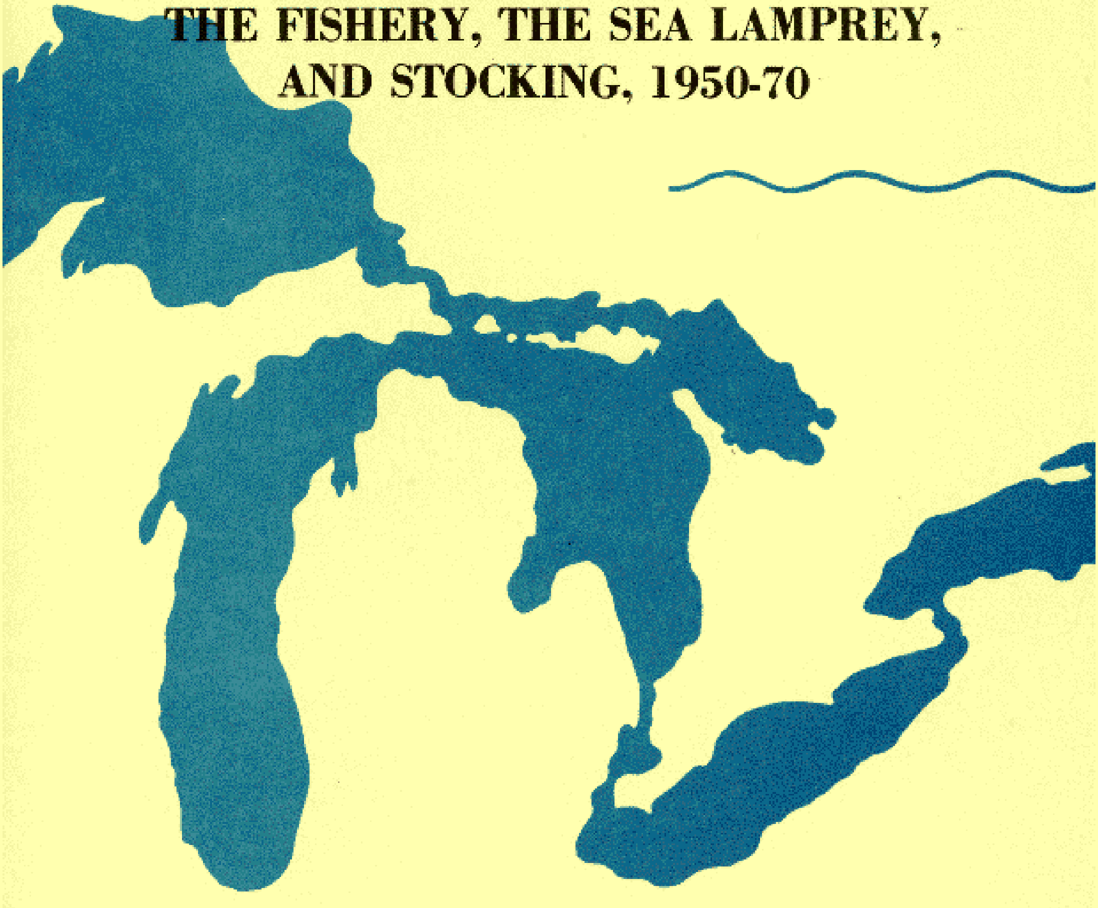
CHANGES IN THE LAKE TROUT POPULATION OF SOUTHERN LAKE SUPERIOR IN RELATION TO THE FISHERY, THE SEA LAMPREY, AND STOCKING, 1950-70



Great Lakes Fishery Commission

TECHNICAL REPORT No. 28

The Great Lakes Fishery Commission was established by the Convention on Great Lakes Fisheries, between Canada and the United States, ratified on October 11, 1955. It was organized in April, 1956 and assumed its duties as set forth in the Convention on July 1, 1956. The Commission has two major responsibilities: the first, to develop co-ordinated programs of research in the Great Lakes and, on the basis of the findings, recommend measures which will permit the maximum sustained productivity of stocks of fish of common concern; the second, to formulate and implement a program to eradicate or minimize sea lamprey populations in the Great Lakes. The Commission is also required to publish or authorize the publication of scientific or other information obtained in the performance of its duties.

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CHANGES IN THE LAKE TROUT POPULATION OF SOUTHERN LAKE SUPERIOR IN RELATION TO THE FISHERY, THE SEA LAMPREY, AND STOCKING, 1950-70

by

RICHARD L. PYCHA
U.S. Fish and Wildlife Service
Ashland, Wisconsin 54806

And

GEORGE R. KING
Wisconsin Department of Natural Resources
Bayfield, Wisconsin 54814

TECHNICAL REPORT NO. 28

Great Lakes Fishery Commission
1451 Green Road
P.O. Box 640
Ann Arbor, Michigan 48107

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DEDICATION

We dedicate this report to the memory of the late Robert W. Saalfeld, Executive Secretary of the Great Lakes Fishery Commission from 1971 until June 9, 1974, and Assistant Executive Secretary from 1957 to 1971. In the earlier years Bob coordinated activities of state, provincial, and federal agencies related to rehabilitation of lake trout stocks in the Great Lakes. Later he dealt mainly with sea lamprey control, contracting of research, and the many administrative functions of the office.

Although Bob had no direct authority over any agency, his influence was felt by almost everyone engaged in rearing, marking, and stocking lake trout; in research on lake trout; and in setting policies and regulations for management of the fisheries. Many of us valued him as a close personal friend. As a coordinator he created a climate that fostered outstanding accomplishments by others. He never sought personal credit.

This report summarizes the lake trout rehabilitation program of the Commission and cooperating agencies in Lake Superior-only part of a broader operation that has yielded immense benefits to fishermen there and in Lake Michigan as well. That success stands as a monument to Bob's memory.

CHANGES IN THE LAKE TROUT POPULATION OF SOUTHERN LAKE SUPERIOR IN RELATION TO THE FISHERY, THE SEA LAMPREY, AND STOCKING, 1950-70[1]

by

Richard L. Pycha and George R. Ring

ABSTRACT

Commercial catch and effort statistics for 1929-70, samples of commercial catches in 1959-62, and records of examinations of all lake trout ***(Salvelinus namaycush)*** taken commercially in inshore waters of Michigan and Wisconsin in 1962-70 were the basis for descriptions of changes in the population in 1929-70.

Abundance fluctuated cyclically and gradually downward in 1929-49, whereas fishing intensity tended to increase during the same period. In 1950-52, a change from cotton to nylon twine in gillnets raised effective fishing effort to 305% of the 192943 average in Michigan waters and to 228% in Wisconsin waters; production held near average. Abundance fell to 18% of average in Michigan in 1953-61 and to 25% of average in Wisconsin in 195661; in the same periods, production fell to 11% of average in Michigan and to 19% in Wisconsin. In 1962-70 abundance rose to 160% in Michigan and 246% in Wisconsin while production and fishing intensity were held low (3-14%) by regulation.

Changes in abundance of Lake trout were attributable to a sequence of developments in successive series of years: intensive fishing in the early 1950's; severe sea lamprey predation in the late 1950's; an 85% reduction in abundance of sea lampreys in mid 1961; and the combination of sea lamprey control, intensive stocking of yearling lake trout, and restrictions on fishing in 1962-70. A decline in average size of lake trout and the near elimination of spawning stocks in 1953-61 curtailed recruitment of native lake trout in the mid 1960's. Stocking of fin-clipped lake trout replaced natural reproduction in the early 1960's. In 1965-70, the lake trout population was composed mainly of hatchery-reared fish. Natural reproduction was reestablished on one major spawning shoal in Wisconsin in 1965, but in 1970 only 10% of the legal (17-inch and longer) and 17% of the undersize lake trout in Wisconsin were native fish.

Reduction of sea lamprey abundance resulted in an immediate increase in survival and abundance of lake trout, especially of the larger sizes. As abundance of lake trout progressively increased in 1962-70, survival of the smaller legal-size lake trout increased, probably due to reduction of the predator-prey ratio and an increase in availability of Larger lake trout preferred by sea lampreys. Abundance of spawning-size lake trout was limited by high natural mortality in 1965-70. Circumstantial evidence suggested that sea lamprey predation contributed a major part of the high natural mortality.

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[1] Contribution 498, Great Lakes Fishery Laboratory, U.S. Fish and Wildlife Service, Ann Arbor, Michigan 48107

INTRODUCTION

The decline of lake trout (Salvelinus namaycush) and other valuable fishes in the upper Great Lakes has been generally attributed to predation by the sea lamprey (Petromyzon marinus). Hile (1949) considered it to be the only significant factor in the decline of lake trout in Lake Huron, and Fry (1953) presented strong evidence that it nearly exterminated lake trout in South Bay, Lake Huron, where commercial fishing had not been permitted for more than 20 years. The sea lamprey was held to be the sole cause of the collapse of the fishery in Lake Michigan by Hile et al. (1951a), but Smith (1968) suggested that an increase in fishing in Illinois waters could possibly have initiated the decline in that lake. Eschmeyer (1957) showed that the population in Lake Michigan continued to decline in the presence of sea lampreys after the fishery collapsed. Although the relative effects of fishing and sea lamprey predation were never determined, the decline of formerly stable fisheries shortly after establishment of sea lamprey populations was strong circumstantial evidence that the imposition of sea lamprey predation upon intensively fished populations caused the declines of lake trout in Lakes Huron and Michigan. Fry's and Eschmeyer's studies indicated that sea lampreys were capable of exterminating lake trout even in the absence of fishing.

The respective roles of sea lamprey predation and fishing in the decline of lake trout in Lake Superior were less clear than in Lakes Michigan and Huron. Sea lampreys established spawning runs in several tributary streams of eastern Lake Superior before 1950, and spread throughout the lake and increased rapidly in abundance during the 1950's. Loftus (1958) showed that mortality of river-spawning lake trout in Ontario waters of eastern Lake Superior increased greatly as the incidence of lamprey scars increased in 1951-55, and concluded that sea lampreys caused the rapid decline in numbers of river-spawning fish. Hile et al. (1951b), however, showed that in Michigan waters of Lake Superior, abundance of lake trout fell from 107% of the 1929-43 average in 1944 to only 77% in 1946, the year the first sea lamprey was reported in the lake, and continued to decline to a record low of 65% in 1949; they pointed out further that the decline in abundance was accompanied by progressive increases in fishing effort to record high levels and warned that the lake trout stocks were in poor condition to withstand the expected ravages of the sea lamprey.

Regardless of the relative importance of the sea lamprey and the fishery as causative factors, steady declines in production that were disastrous to the Lake Superior fishery began in 1951 in Ontario and Michigan, in 1953 in Minnesota, and in 1956 in Wisconsin (Baldwin and Saalfeld 1962). Lakewide production dropped from a 4.7 million pounds in 1949 to 371,000 pounds in 1961-a 92% decline in little more than a decade. No measures were taken to reduce or curtail fishing during the decline because the evidence from Lakes Huron and Michigan indicated that lake trout were doomed unless the sea lamprey was controlled.

Effective control of sea lampreys became possible with the development of a selective chemical that destroyed lamprey larvae in streams (Applegate et al. 1961). After all known sea lamprey-producing tributaries of Lake Superior were treated with the larvicide in 1958-60, abundance of parasitic-phase lampreys abruptly fell about 85% in mid 1961 (Lawrie 1970).

When development of the selective larvicide made sea lamprey control feasible, large-scale stocking of fin-clipped lake trout was begun in the hope that lake trout stocks would be rehabilitated quickly after lamprey control became effective. Nearly all the fish were stocked as yearlings because experimental plantings of fin-clipped and tagged lake trout in the early 1950's had indicated this to be the best age for release (Buettner 1961). Stocking was increased rapidly after 1957 and was intensive throughout the 1960's.

The Fisheries Research Board of Canada, the Wisconsin Department of Natural Resources, and the U.S. Fish and Wildlife Service began intensive sampling of commercial lake trout catches in Ontario, Wisconsin, and Michigan in 1958-59 (the fishery in Minnesota had collapsed almost completely by 1959). In mid 1962, commercial lake trout fishing was banned in all U.S. waters, except for a small amount continued for scientific purposes by selected "assessment" fishermen under contracts or permits. The fishery was not closed in Ontario, but was restricted to area quotas large enough to provide fish for the needed biological information.

The program to control the sea lamprey and restore the lake trout population of Lake Superior involved work by state, provincial, federal, and international agencies. Sea lamprey control and research were carried out by the U.S. Fish and Wildlife Service and the Fisheries Research Board of Canada (now the Canadian Department of the Environment) under contract to the international Great Lakes Fishery Commission. Lake trout research, development of hatchery brood stocks, and rearing and stocking of lake trout were done by state, provincial, and federal conservation agencies; the work was coordinated by the Commission. Fishery regulation is the responsibility of individual state and provincial conservation agencies. Coordination of management policies was achieved to some degree through committees organized under the auspices of the Commission. This loose assemblage of agencies was able, by cooperative effort, to develop lake trout brood stocks and rearing facilities during the late 1950's in anticipation of control of the sea lamprey; to act 'decisively when protection of lake trout stocks was recommended by the Commission in 1962; and to maintain assessment fisheries for biological sampling through 1970.

We describe here the major changes in the lake trout population in southern Lake Superior during the period of maximum decline (1950-61) and the first 9 years of recovery (1962-70), with particular emphasis on the 12 years, 1959-70. We also describe associated changes in the fishery, the sea lamprey population, and stocking rates and examine their relations to the lake trout population.

LAKE TROUT POPULATION AND FISHERY

Characteristics of the population

The lake trout population of Lake Superior is composed of an unknown number of subpopulations. Two forms have commonly been given subspecific ranking, the "lean" or typical lake trout *(Salvelinus n.*

namaycush) and the siscowet or “fat” trout *(Salvelinus n. siscowet).* Several, perhaps many, races exist within these groups.

Lean lake trout are found in inshore waters and on the banks of most offshore islands, generally at less than 50 fathoms. They have the fastest growth rate of any of the main subpopulations of lake trout in Lake Superior (usually 3-4 inches per year-Rahrer 1967), mature at a relatively advanced age and large size (generally at ages VII-IX and a length of 25 inches or longer for females-Eschmeyer 1955), have a long life span (28 years in a hatchery-Eschmeyer 1964) and some grow to large sizes (the angling record is 63 pounds, 2 ounces, and larger fish have been taken commercially). They congregate for spawning from late September through early November. Most spawning is in mid to late October on rock and rubble reefs at depths of l-10 fathoms, but storms occasionally force them to move deeper and spawn at depths down to 20 fathoms. Several subpopulations of lean lake trout spawned in Ontario rivers tributary to eastern Lake Superior (Loftus 1958) but some of these groups may now be extinct.

The siscowet is concentrated on steep banks in deep water (generally 50-120 fathoms) in many areas throughout the lake. Although relatively little has been published on the life history of the siscowet, unpublished data and field observations indicate that its growth is somewhat slower than that of lean trout and length at maturity is shorter (probably 22-23 inches). Siscowets also reach a large size (fish weighing 25-30 pounds were not uncommon). They spawn on reefs, generally (but not always) in deeper water (usually 20-50 fathoms) than do lean trout. Spawning season varies greatly; various races spawned on dates extending from June to late November in the early 1950’s (Eschmeyer 1955). The fat or oil content of the flesh of siscowets increases with length and ranges up to nearly 80% for large specimens. The smaller, less oily siscowets usually bring a higher price than large siscowets and are called “halfbreeds” by commercial fishermen (Eschmeyer and Phillips, 1965).

Lake trout of a third group, not recognized by taxonomists, are called “humpers” or “paperbellies” by commercial fishermen. They are found on isolated reefs or “humps” near Isle Royale, Caribou Island, and on Superior Shoal (Fig. 1). They can be distinguished from lean lake trout and siscowets by a “paper-thin” abdominal wall, and by head and body shape and coloration (Rahrer 1965). The relation between body length and fat content is different from that of lean trout or siscowets (Eschmeyer and Phillips 1965). Humpers grow very slowly (1.5-2.5 inches per year) and mature at a small size (63.2% of females were mature at 15.0-15.9 inches (Rahrer 1965). Either they rarely grow to a length greater than 25 inches, or longer humpers have been marketed as siscowets. They spawn in August or September on or near the tops of the reefs they inhabit all year. Limited data on returns of humper trout tagged near Isle Royale indicate they move little and that intermixing of the subpopulations is almost nil (unpublished records of the Ashland Biological Station). Tagging studies on Superior Shoal in Ontario waters confirm this observation (A. H. Lawrie, personal communication). In Ontario, humper and “halfbreed” trout are sometimes called “bankers” by commercial fishermen.

The studies of Loftus (1958) on river-spawning lake trout, and those of Eschmeyer (1955) and Rahrer (1968) on lake-spawning fish indicated that

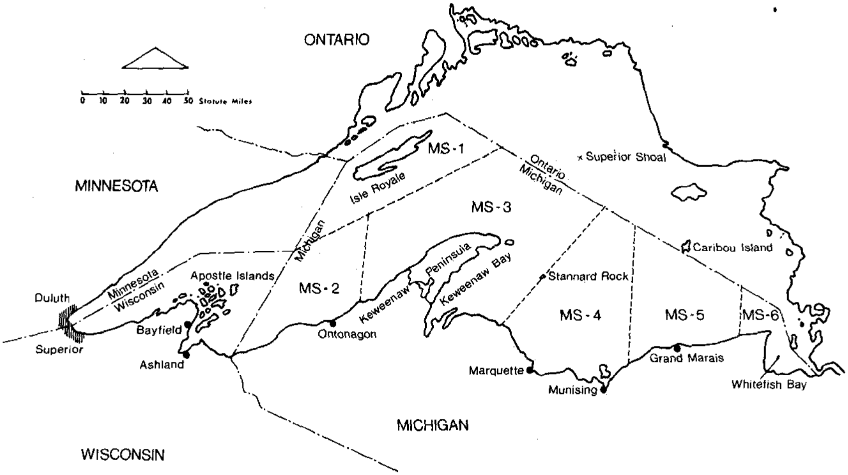

Figure 1. Lake Superior, showing statistical districts and localities mentioned in the text.

lean lake trout disperse widely between spawning seasons but have a strong tendency to return to the same sites to spawn in successive seasons. The evidence for homing of lean trout, the sedentary nature of humper trout, and the great variation in time of spawning among different groups of siscowets suggest that the lake trout population of Lake Superior is composed of a large number of races that are partially or wholly isolated during spawning, but intermingle to various degrees between spawning seasons.

Some, possibly many, of the races of lake trout in Lake Superior became extinct in 1959-61. Generally, abundance of the deepwater siscowet and offshore humper trout declined less during that period than that of the inshore lean trout. Whether the races of lean lake trout differed significantly in characteristics other than spawning locally is unknown.

Details on fishing methods and procedures are given in the following two sections.

Fishing methods

Several types of gear and methods of fishing were employed in the commercial fishery.. Since 1929, when data on gear and fishing effort became available, the largemesh (4 1/2- to 7-inch, stretch-measure) gillnet was the gear most commonly used. During most of the year, 4 1/2-inch nets set on the bottom were used in most areas, but Larger-mesh nets were fished at less than 20 fathoms for spawning concentrations. of large lake trout in late September and early November. (The season was closed during all or most of October in all U.S. waters.) Longlines with baited hooks, usually suspended by floats at about 30 feet from the surface in 70-80 fathoms of water, produced many lake trout in the 1930’s, but their use diminished in the 1940’s and almost none were fished after 1955. These “‘float hooks,” which were fished in April-July, caught much larger lake trout than gillnets fished on the bottom. Some “bottom hooks” were fished in Wisconsin waters. A few fishermen fished “float nets” (large-mesh gillnets suspended like the longlines), especially in the nearshore waters around Isle Royale. Large-mesh gillnets were also fished on bottom under the ice in the Apostle Islands region of Wisconsin Pound nets and trap nets were fished in several areas where lake whitefish (Coregonus *clupeaformis*) and lake trout could be taken together. Although their use declined with the general depression of the industry in the 1950's, pound nets were still being used in the Apostle islands region in 1970, and trap nets were still in use near Marquette, Michigan, and in Whitefish Bay. Small-mesh (2 1/2- to 3-inch) gillnets fished for other species, trolling, and "bobbing" (jigging through the ice) accounted for a very small portion of the total commercial catch.

Changes in materials that affected the efficiency of gillnets were made during the years (1929-70) when fishing effort data were collected (Pycha 1962). In the 1930's cotton twine largely replaced linen twine. The more elastic cotton twine was probably slightly more efficient than linen, but the difference was apparently not great (quantitative data are not available). In the late 1940's, some fishermen began using cotton twine so fine the nets were called "spider webs." These nets were reputed to have been as efficient as the nylon nets that replaced them, but few fishermen used them because they were not durable. The fast spun nylon nets were used in late 1949, and by 1952 nearly all nets in use were of this material. The common 4 1/2-inch-mesh nets were about 2.25 times as efficient as the typical cotton nets of the 1940's (Pycha 1962). A few monofilament nylon nets were fished in the early 1960's but they never came into general use.

Gillnets were commonly fished for 5-7 nights in the spring and in late fall and winter. As the water warmed in the summer, they were fished for shorter periods; 2- and 3-night sets were common in September, when the water was warmest.

Minimum size limits for lake trout were imposed through Lake Superior. In Wisconsin, the minimum legal size was 17 inches (total length). In Michigan, legal sire was based on weight (1 1/4 pounds, dressed) through 1967, but was changed to 17 inches in 1968. (In terms of size of fish, the two values were nearly identical.)

Assessment methods

All assessment fishing under contract or permit in 1959-70 was done with spun nylon gillnets, nearly all of which were 4 1/2-inch mesh, set on the bottom. Some 6-inch mesh float nets were fished off southern Isle Royale in the manner traditional to that area. Catch and effort data from this fishery were used for computation of the indices of production, abundance, and fishing intensity, but data on size composition were not included with those from other areas. Biologists sampled pound-net catches in Wisconsin, but only enough to determine that the size composition was almost identical to that of catches from 4 1/2-inch-mesh gillnets.

Methods of sampling commercial lake trout catches in 1959-62 were described by Pycha and Ring (1967). The same methods were used from mid 1962 through 1970, but the amount of fishing was restricted, and all lake trout were measured (to the nearest 0.1 inch, total length) and checked for clipped fins and lamprey wounds or scars. Scale samples were taken periodically. Data were recorded on amount of gear, depth, and location of fishing; number of legal-size and dead undersize fish; and weight of legal catch. Live undersize fish were returned to the lake immediately and no data were recorded for them. Fish lengths were summarized by l-inch groups for computations The study is based primarily on lean lake trout taken in waters near the south shore and the adjacent islands of southern Lake Superior.

Data on commercial fishing effort and landings were collected by the Michigan and Wisconsin Departments of Natural Resources and were compiled by the U.S. Fish and Wildlife Service at the Great Lakes Fishery Laboratory, Ann Arbor, Michigan. Although indices of production, abundance, and fishing intensity were based on catch and effort data for all Michigan and Wisconsin waters, and thus included landings of siscowets and humper trout from deep and offshore waters, total production of groups other than typical lean trout was not large enough to affect the indices greatly.

Hile (1962) and Pycha (1962) both concluded that little purpose would be served by publishing lake trout abundance indices corrected for use of nylon nets in the 1950's because the fishery appeared unlikely to ever return to its former character or magnitude. Nevertheless, an index of lake trout abundance was needed to follow the progress of stock rehabilitation, and comparisons of abundance in the 1960's with that in the years before the invasion of the sea lamprey and use of nylon nets (pre-1950) could not be avoided. In calculating indices of abundance and fishing intensity for 1950-70 we used corrections and adjustments of data that preserve reasonable comparability with the indices for 1929-49 published by Hile et al. (1951b).

The indices of production, abundance, and fishing intensity for Michigan waters in 1929-49 are from Hile et al. (1951b), and follow the terminology and methods given by Hile (1962). The change from a multiplegear fishery in 1929-49 to an essentially single-gear (large-mesh gillnet) fishery by the mid 1950's precluded the need to consider catches from several types of gear after 1949. Although use of gears other than gillnets declined in the 1940's, the other gears still accounted for 23% of the total production of lake trout in 1949. Thereafter the use of other gears declined rapidly and in 1956-70 large-mesh gillnets accounted for more than 96% of the production. Abundance indices for 1950-70 were calculated only from the annual average catch (pounds) per unit (1,000 linear feet) of large-mesh gillnet. All gillnet effort in 1952-70 was adjusted upward by the 2.25 efficiency factor of nylon to cotton twine for calculation of catch per unit effort (CPE). It was assumed (on the basis of conversations with many commercial fishermen) that one-fourth of the gillnets fished in 1950 and one-half of the nets fished in 1951 were nylon.

Selected "assessment" fishermen provided data on their catches in 1959 through mid 1962 and were the only fishermen who fished for lake trout in inshore waters from mid 1962 through 1970. Most of the assessment fishermen were selected because they had been major producers of lake trout. Comparisons of their annual average CPE's in 195961 with the average CPE's for all fishermen in their statistical districts showed clearly that all but one of the assessment fishermen were more efficient than the average for their districts.

Several adjustments were made in data for 1963-70 to maintain comparability with data from earlier years. CPE's of assessment fishermen were adjusted to "average" by application of factors derived from the relation of their average CPE's to the average CPE for all fishermen in their statistical districts in 195961 before the commercial fishery was closed. In 1967-70, several additional assessment fishermen were allowed to fish under permit in offshore waters of districts MS-5 near Caribou Island and MS-l near Isle Royale. Catches by these "new" assessment fishermen were included in production summaries, but abundance indices were based only on the records of "old" assessment fishermen who fished those areas. Because CPE was typically much higher in offshore than in inshore waters of MS-S, the increase in production in offshore waters in 1967-70 sharply increased the average CPE for the district. An adjusted average CPE was derived by calculating separate CPE's for inshore and offshore waters which were then combined by weighting each according to the proportion of production in the two areas in 1959-60, before the fishery was closed,

The corrected and adjusted-CPE values for each statistical district were then expressed! as percentages of the 192943 district means and were weighted and combined to form a single index for Michigan waters in the manner of Hile (1962). Since no assessment fishing was done in district MS-2 in 1963-70 and no fishing was done by the "old"' assessment fishermen in MS-1 in 1969-70, weighting factors that excluded these districts were applied for the appropriate years.

The indices of production are simply total production expressed as percentages of the 1929-43 average total production.

The indices of intensity were calculated from the relation: total production index X 100/combined abundance index = percentage intensity. Although this method of calculation yields an index that is not identical with the "intensity" index defined by Hile (1962), the differences between the two indices (as applied to the lake trout fishery) were, at most, only a few percentage points. Such small differences are of no significance in view of the large changes in the fishery in 1950-70. Use of the term "‘intensity" is retained only because 1929-49 data of Hile et al. (1951b) are included in this study.

Data from Wisconsin waters were treated in essentially the same manner as those from Michigan, but data on effort were not available for the 1929-43 base period used by Hile et al. (1951b) for Michigan waters (edited and compiled data were available only for 1949-70). Summaries made by the Wisconsin Department of Natural Resources-indicated that the CPE in Wisconsin waters in 193748 was almost identical to that in the adjacent Michigan district MS-2. The 1929-43 mean CPE in MS-2 was therefore used as-the base for-calculation of abundance indices in Wisconsin for 1949-70.

The indices calculated from the corrected and adjusted data are by no means unbiased. Several unavoidable biases remain and, for some, only the direction of the bias is known. Possible underestimation of abundance may be due to: (1) Calculation of abundance indices from gillnet CPE alone (this bias was small for 1950 [1.5%] and was almost nil for 1956-70). (2) Reduction in the number of nights between lifts of the nets in the spring, as abundance rose in 1962-70 (from 5-7 nights in 1962 to 3 nights in 1968-70). (3) The assumption that all nets fished in 1952-70 were nylon (a few cotton nets were still fished into the mid 1950's). Possible biases toward overestimation of abundance were probably much greater than those toward underestimation and included: (1) Use of finetwine "spider web" nets by some fishermen in the late 1940's. (2) Progressive reduction or cessation of operations by fishermen at times of the year when availability was low in 195261. (3) Drastic reduction of fishing effort in 195262, which reduced gear competition. (4) Abandonment of certain grounds and complete cessation of fishing by many, possibly less efficient, fishermen. (5) Cessation (due to decreases in size of lake trout in the population) of the float hook and float net fisheries that caught large pelagic lake trout. (6) The effects of these size changes on vulnerability to 4 1/2-inch bottom nets.

Had the monthly distribution of fishing effort in 1959 been the same as it was in 192943, the 1959 average CPE would have been lowered about 15%. Gear competition (types 2 and 3 of Ricker 1958) probably existed during the 1940's and 1950's but its reduction could not be quantitatively evaluated. When the fishery was closed in 1962, CPE's of the few remaining assessment fishermen did not increase immediately. The effects of abandonment of certain grounds and attrition of fishermen are not entirely clear. Individual fishermen tended to concentrate a greater proportion of their effort on the better grounds within their usual areas of operation as abundance and effort declined. However, effort was reduced more on some of the best grounds in the lake than on others because many of the best grounds were far from ports and were fished only by large, efficient operators who were forced by adverse economic factors to cease operations Many factors besides fishing skis, such as family ties, age of the fisherman (younger men tended to leave the industry first), size of the operation, and business acumen (some survived by establishing local retail markets) were involved in attrition of fishermen.

In late spring and early summer many of the larger lake trout in the population rise off the bottom and are pelagic over deep water. The float hook and float net fisheries were dependent on these large trout. As abundance and average size of lake trout declined in the 1950's, the fisheries for pelagic lake trout collapsed. Probably a greater proportion of the population was composed of sizes that remained near bottom, where they were vulnerable to the bottom nets.

As abundance of lake trout rose in 196267, the imposition of fixed sampling quotas resulted in reductions of fishing effort that made estimates of abundance progressively less reliable (in 1968-70, effort was held at about the 1967 level). Confidence limits (95%) for the mean annual CPE's of individual fishermen indicated that sampling errors should usually have been no greater than 15%. Errors in the abundance indices (based on combined data from ah fishermen) due to sampling alone should be less than 15%.

State of the stocks, 1929-70

In their analysis of the commercial lake trout fishery in Michigan waters of Lake Superior in 192949, Hile et al. (1951b) showed that, in contrast to the relation in most other Great Lakes fisheries, abundance and

Table 1. Production, abundance, and fishing intensity for lake trout in Michigan and Wisconsin waters of Lake Superior, 1929-70 (Expressed as percentages of the 1929-43 means).

Year	Michigan			Wisconsin		
	Production	Abundance	Intensity	Production	Abundance	Intensity
1929	93	108	86	103	–	
1930	83	101	82	87	–	
1931	95	100	93	91	–	
1932	96	103	91	104	–	-
1933	83	117	72	103	–	-
1934	121	137	86	113	–	
1935	126	111	111	92	–	
1936	113	106	104	96	–	-
1937	111	95	115	81		-
1938	106	86	123	96		-
1939	94	81	115	85	-	-
1940	89	80	109	94		-
1941	91	82	109	116		-
1942	98	91	106	121	-	-
1943	101	102	99	114	-	-
1944	131	107	122	130	-	-
1945	124	98	124	106	-	-
1946	126	77	163	98	-	
1947	108	80	132	95	-	-
1948	105	70	148	102	-	-
1949	106	65	162	95	92	103
1950	116	62	188	109	83	131
1951	105	47	224	93	71	131
1952	101	33	305	96	42	228
1953	85	32	265	83	44	188
1954	78	29	269	80	38	211
1955	67	30	223	102	51	200
1956	59	28	212	88	41	215
1957	41	26	158	53	37	143
1958	38	27	141	48	41	116
1959	32	25	127	34	31	118
1960	13	18	73	20	25	80
1961	11	18	59	19	27	70
1962	6	23	28	22	48	46
1963	3	22	14	7	55	13
1964	3	27	12	8	70	11
1965	3	34	10	10	89	11
1966	4	42	9	10	92	11
1967	7	60	11	10	102	10
1968	8	98	8	7	…	…[a]
1969	9	134	6	4	146	3
1970	6	160	4	9	246	4

[a] No comparable data because of changes in sampling methods.

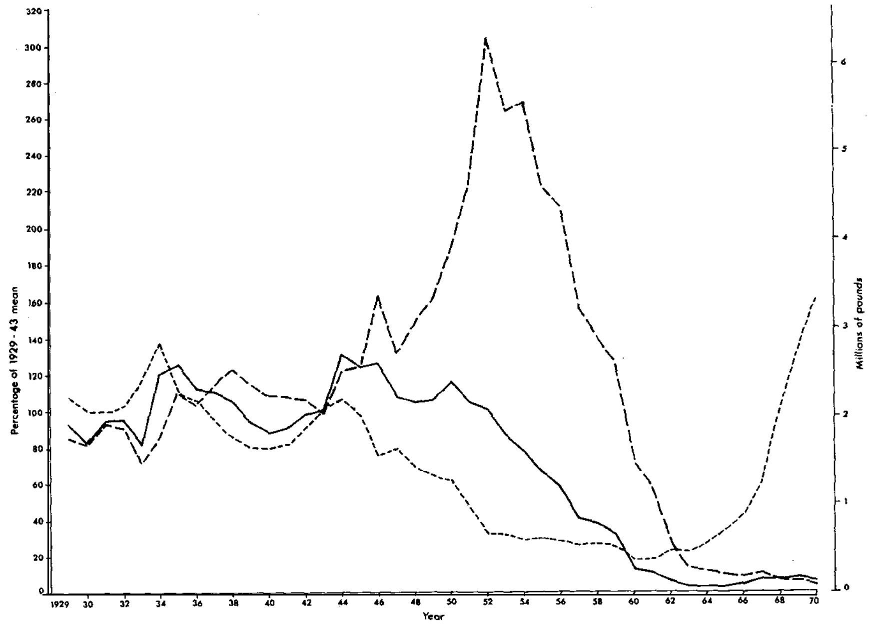

Figure 2. Commercial fishery statistics for lake trout in Michigan waters of Lake Superior, 1929-70: production (solid line), abundance (short dashes), and fishing intensity (long dashes) are expressed as percentages of the 1929-43 means (scale at left); production in pounds is shown by scale at right. (Data for 1929-43 are from Hile et al. [1951b] .)

fishing intensity fluctuated inversely (Table 1, Fig. 2). Abundance fluctuated between highs of 137 and 107% of the 1929-43 average in 1934 and 1944 and lows of 80 and 65% in 1940 and 1949. The trend of abundance was distinctly downward and that of fishing intensity was definitely upward. Although Hile et al. (1951 b) only speculated that increasing fishing pressure and declining abundance might have been causally related, they warned of the precarious status of the fishery in 1949.

In 1949-52 the trends in production, fishing intensity, and abundance were continued or intensified. Adjustments made in the data to allow for the conversion from cotton to nylon gillnets in 1950-52 increased the fishing intensity index from 162 in 1949 to 305 in 1952. The abundance index fell from 65 in 1949 to only 33 in 1952. Production remained slightly above the 1929-43 average of 2.1 million pounds.

Low and steadily declining abundance of lake trout in 1953-61 resulted in near collapse of the Michigan fishery before the mid 1962 closure, but abundance recovered sharply in 1962-70. Production fell from an index of 101 in 1952 to only 11 in 1961 and was held between values of 3 and 9 in 1962-70. Intensity fell from a value of 305 in 1952 to only 59 in 1961. It was reduced to 28 by the midseason closure of fishing in 1962 and was held between 4 and 14 by regulation in 1963-70. Abundance declined gradually

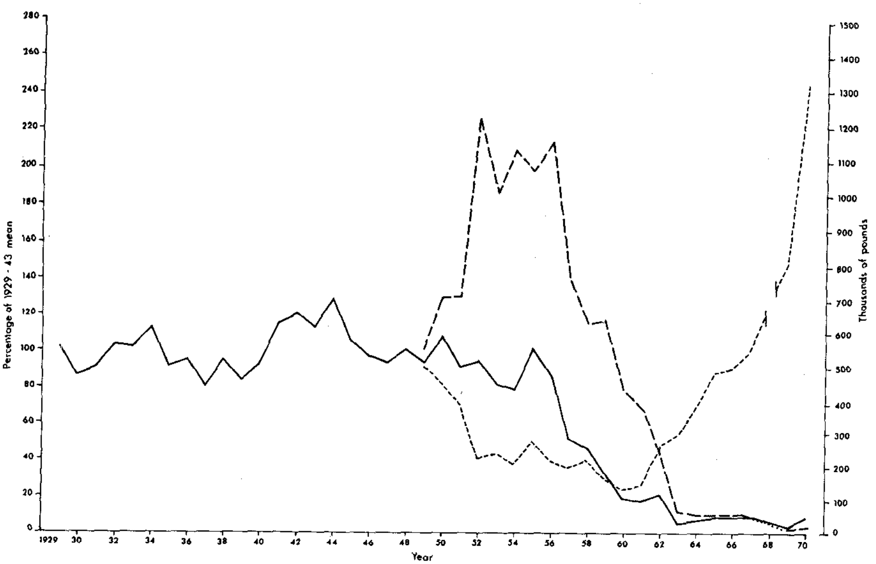

Figure 3. Commercial fishery statistics for lake trout in Wisconsin waters of Lake Superior, 1929-70: production (solid line), abundance (short dashes), and fishing intensity (long dashes) are expressed as percentages of the 192943 means (scale at left); production in pounds is shown by scale at right. (The abundance indices are based on the 1929-43 mean in Michigan district MS-2; see text for explanation.)

from an index of 33 in 1952 to only 18 in 1960. It remained at 18 in 1961, increased slightly in 1962-63, and then increased steadily and rapidly from an index of 22 in 1963 to 160 in 1970.

Fluctuations in commercial production in Wisconsin in 1929-49 were similar to those in Michigan (Table 1, Fig. 3), but production, fishing intensity, and abundance were still near the 1929-43 average in 1949 (mean production was 543,000 pounds). Production fluctuated irregularly downward in 1949-54, increased sharply to average in 1955 (index 102), and was still at an index of 88 in 1956. The effort adjustment for nylon nets resulted in a sharp rise in fishing intensity, from an index of 103 in 1949 to 228 in 1952. Intensity remained near or above an index of 200 through 1956. The abundance index fell from 92 in 1949 to 42 in 1952 and fluctuated without trend near this level through 1956.

After 1956, the Wisconsin fishery declined disastrously. Production fell from an index of 88 in 1956 to only 19 in 1961. It rose slightly to 22 in 1962 in spite of the midseason closure of fishing, but was held at indices of only 4-10 by regulation in 1963-70. Intensity fell from an index of 215 in 1956 to 70 in 1961, was reduced to 46 by the mid 1962 closure of fishing, and was held at values of 3-13 by regulation in 1963-70. Abundance fell from an index. of 41 in 1956 to its low of 25 in 1960. It recovered slightly to 27 in 1961 (due to a sharp increase in the fall of that year) and rose rapidly and steadily to an index of 246 in 1970.

Owing to biases discussed earlier, the decline of abundance of lake trout was probably somewhat steeper than described for 1948-50 in Michigan waters and for 1954-61 in both Michigan and Wisconsin. Although the 1962-70 abundance indices are probably serious overestimates, they are all reasonably comparable, and the rapid rise in abundance was real. Experimental fishing, special assessment fishing on grounds other than those regularly fished, and incidental catches of lake trout in nets set for lake whitefish all indicated that the high abundance was not due to concentrations of fish in a few areas, but was general in most areas along the south shore of the lake. Even when allowance is made for substantial error for bias, the 1970 abundance index was higher than at any time since the early 1930's for Michigan waters and was probably higher than at any time in the previous 40 years for Wisconsin waters.

Even though abundance was near record high levels in both Michigan and Wisconsin in 1970, the potential yield could be greatly different from that before 1950. When the lake trout fishery was operating near maximum equilibrium yield as it was before 1950 (Sakagawa and Pycha 1971), the abundance index indicated the density of legal-sized fish on the grounds while removals were being offset by recruitment. The high abundance indices in 1970, however, reflected the accumulation of planted stocks for several years, during a period when removal by the commercial assessment fishery was held very low by regulation.

The data of Table 1 and Fig. 2 suggest that the decline in abundance of lake trout in Michigan waters in the late 1940's and early 1950's was caused mainly by increasing fishing intensity. Hile et al. (1951b) believed that the abundance index in 1949 was still within the possible range of normal natural fluctuations even though it was a record low. The decline in production in 1951-52, which occurred in spite of the large increase in intensity, certainly indicated that fishing pressure was too high. By 1951 abundance had fallen too low to be attributed to a normal fluctuation in what had been a very stable fishery for several decades. The data for Wisconsin waters (Table 1, Fig. 3) suggest that the somewhat smaller increase in intensity there may have resulted in establishment of a new but temporary equilibrium between the stocks and the fishery in 1952-56.

The data of Table 1 and Figs. 2 and 3 also suggest that abundance of lake trout was not controlled by the fishery in the late 1950's and early **1960's. Abundance declined more rapidly than in the mid 1950's in** spite of drastic reductions in fishing effort. Although the abundance indices calculated from annual average CPE values do not illustrate it, abundance fell to its lowest point in the spring of 1961 and rose sharply in the following fall and early winter. The higher abundance persisted through the spring of 1962 before the fishery was closed. In Wisconsin, the increase was large enough to support production in the first half of 1962 greater than that throughout 1961. Most of the data for the 1962 Wisconsin abundance index were from spring catches made while the fishery was open. During that period fishing intensity was considerably higher than in the spring of 1960 or 1961. The reversal of the downward trend in abundance of lake trout was, therefore, unrelated to changes in fishing intensity in the early 1960's.

THE SEA LAMPREY

Life history

The life history of the sea lamprey in Lake Superior is closely similar in most details to that of the lamprey in the other Great Lakes, as described by Applegate (1950). Most newly transformed adults are believed to move downstream to the lake in late fall in the Lake Superior drainage (Patrick J. Manion, manuscript in preparation) rather than in spring as reported by Applegate (1950) and Applegate and Brynildson (1952) for northern Lakes Huron and Michigan. Field conditions in winter and early spring are so severe in the Lake Superior drainage, however, that it is extremely difficult to make accurate observations. The newly transformed adults that move downstream into Lake Superior in the fall remain there for 16-20 months and enter spawning streams in April-July (mainly in late May and early June in the Lake Superior drainage).

The parasitic phase of the sea lamprey's life history in Lake Superior is incompletely known. Most of our information comes from field observations made before 1962, when lampreys were abundant. In the late 1950's, many commercial fishermen reported catching hundreds of small (5 1/2- to 6 1/2-inch) recently transformed lampreys attached to lake herring (Coregonus artedii) during herring spawning runs in late November and early December. These small lampreys made no readily detectable wounds on the herring. From mid December to mid July extremely few small lampreys or fish with small lamprey wounds were observed; we have virtually no information on the location or prey of small parasitic-phase sea lampreys during that 7-month period. All lampreys seen on lake trout in the winter and spring were mature prespawning adults 10-24 inches long (average, about 17 inches) and fresh wounds on lake trout were large. Very few lampreys were seen on lake trout in late June and early July. By late July, feeding lampreys 10-13 inches long were caught attached to lake trout. All fresh wounds on lake trout taken in late July were small. The size of lampreys and the size of wounds on lake trout increased in August and September, and by late October the lampreys seen on lake trout were nearly as large as those in the spring spawning runs. The greatest numbers of large lampreys seen were on whitefish and lake trout caught in December near the mainland shore. Although fewer lampreys of all sizes were seen after 1962, more recent observations match those during the earlier period.

The incidence of fresh wounds on lake trout, siscowets, and the larger humper trout caught at Stannard Rock, Isle Royale, Caribou Island, and Superior Shoal (Fig. 1) indicates that substantial numbers of sea lampreys reach these remote areas. How they reach these areas and how long they remain there are unknown.

Abundance

Information on abundance of sea lampreys in Lake Superior is lacking for the early years of the invasion; later it was obtained from counts at electrical barriers that were installed in tributary streams to prevent adults from reaching their spawning grounds. Information on lamprey counts at the barriers was published by Smith et al. (1974). The first sea lamprey was reported in 1946, but no measure of abundance of lampreys was available until 1953, when electrical barriers and traps were installed in 11 streams along the eastern third of the south shore (5 of these were later designated as index streams for annual counts of lampreys in spawning runs.) Additional barriers were constructed in other streams as soon as it became known that sea lampreys spawned in them; by 1958, a total of 45 barriers and traps were in operation along the south shore (McLain et al. 1965), and a system of barriers was in operation along the Canadian shore (Lawrie 1970). After the treatment of streams with larvicide proved to be an effective control measure, the number of barriers was reduced; barriers were operated in 16 index streams for assessment of abundance of lampreys in 1963-70.

If construction of barriers had kept pace with the spread of the sea lamprey, the total catches of lampreys at the 16 index-stream barriers (or as many of the 16 as were in operation in 1953-57) would represent comparable estimates of abundance in all years, 1953-70. Reports of local residents to crews constructing the first barriers in Wisconsin, however, suggest that barrier construction did not keep abreast of the spread of the lamprey in Wisconsin; lampreys may have been present there several years before barriers were installed (Smith et al. 1974). Catches of sea lampreys at index-stream barriers in Michigan in 1953-57 probably represent reasonable estimates of relative abundance of lampreys during their initial increase in Michigan waters of the lake, but barrier counts may not give a true picture of the increase of sea lampreys in Wisconsin waters. Other errors in estimation of sea lamprey abundance were caused by variations in weather. In 1960, particularly, floods prevented operation of the barrier traps during most of May just before the peak of the spawning run; consequently that year's count was scarcely indicative of lamprey abundance.

Despite some deficiencies of the data, catches of sea lampreys at the 16 index-stream barriers, or at those operating in 1953-57, are the most comprehensive record of relative abundance available. The total catch increased rapidly in 1953-58, declined in 1959-60, reached its highest point (66,701) in 1961, and fell sharply to 8,826 in 1962 (Table 2). The 1962 decline reflected a reduction in the lamprey population that occurred in mid 1961, immediately after the 1961 spawners entered the streams. Catches in 1962-70 ranged from 7 to 23% of the 1958-62 mean; they were smallest in 1967 in both Michigan and Wisconsin.

Predation on lake trout

Sea lamprey predation on lake trout is not well understood because, with few exceptions, only the survivors of lamprey attacks are seen in the field. The survivors bear marks ranging from open bleeding wounds to scars that are completely healed. The time required for healing is unknown and probably varies greatly. An aquarium study of sea lamprey feeding by Lennon (1954), one of the few sources of information on the mechanism and effects of sea lamprey attacks, includes little information on healing of wounds.

Table 2. Numbers of adult sea lamprey caught at electrical barriers in index streams tributary to Michigan and Wisconsin waters of Lake Superior, early April to July, 1953-70.[a]

Year	Michigan	Wisconsin	Total
1953	1,419		1,419
1954	4,224	-	4,224
1955	9,720	-	9,720
1956	20,757	-	20,757
1957	31,213	19,329 (b)	50,542
1958	22,252	34.996	57,248
1959	20,276	23,829	44,105
1960	22,825	13,418	36,243
1961	35,980	30,721	66,701
1962	5,610	3,216	8,826
1963	7,267	3,597	10,864
1964	4,772	6,995	11,767
1965	4,922	6,915	11,837
1966	3,580	1,181	4,761
1967	2,779	583	3,362
1968	5,109	2,827	7,936
1969	4,366	4,958	9,324
1970	3,774	1,916	5,690

[a] The numbers of barriers in operation were 5 in 1953, 11 in 1954, 13 in 1955, 13 in 1956, and 16 in 1957-70.

Catch does not represent entire run. An experimental barrier installed in the Brule River for testing was not fully effective.

Relatively few lake trout shorter than 16 inches bore fresh lamprey wounds in Lake Superior even when sea lampreys were abundant; among larger fish the percentage with wounds increased rapidly with increase in length. Typical examples of this relation are shown in Figs. 4 and 5. In the spring of 1961, when sea lampreys were at peak abundance and lake trout had become relatively scarce, the percentage of lake trout bearing wounds in Michigan waters increased from nil at about 13.5 inches to 45 at 26.5 inches (values taken from the curve of Fig. 4). Few fish survived to lengths greater than 26.5 inches. In the spring of 1970, when abundance of sea lampreys was much lower and that of lake trout was much higher than in 1961, the percentage wounded increased from nil at about 18 inches to 9.5 at 26.5 inches and 15.5 at 30.5 inches (Fig. 5). The percentages in Michigan waters in other years of 1959-70 were similar to, and fell between, those in Figs. 4 and 5. Pooling data from several l-inch intervals to obtain 20 or more fish for each of the points at the upper end of the length range obscured sharp decreases in wounding rates of the largest fish in most years (the upper points in Fig. 5 illustrate the beginning of this typical trend). The few largest fish in the catch usually bore no lamprey wounds, even in years when the overall wounding rate was very high. The sharp decline in wounding rate occurred only among fish in the upper 3-5 inches of the length range and may have been due to small-sample error alone. Its persistence in most years and seasons, however, leads us to believe the declines are real.

The relations of length of fish to percentage wounded in Wisconsin waters were closely similar to those in Michigan waters in 1959-61, but in

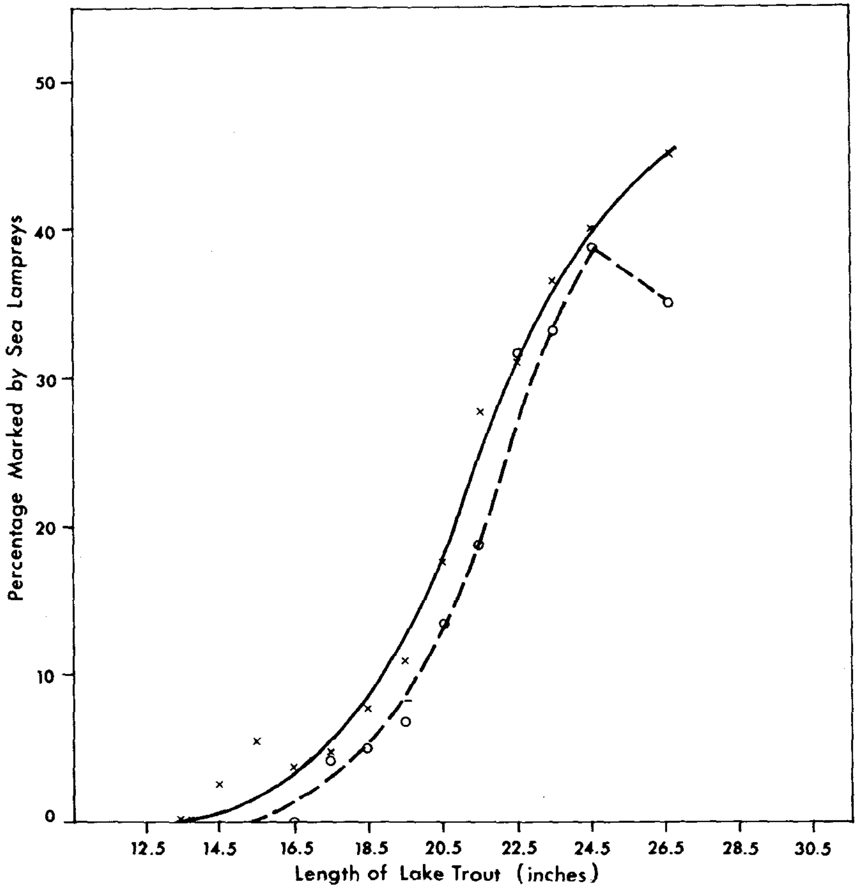

Figure 4. Percentage of lake trout of various lengths bearing **sea** lamprey wounds (solid line) and scars (dashed line) in Michigan waters east of the Keweenaw Peninsula, April-May 1961. (All points represent 20 or more fish. Curves fitted by inspection.)

1962-70 the percentage wounded at any length was much lower than in Michigan. The relation in Wisconsin in most years of 1962-70 was similar to that in the spring of 1968 (Fig. 6), when the percentage wounded rose from nil at about 17.5 inches to only 3 at 26.5 inches and 7 at 30.5 inches.

The increase in wounding rate with length of lake trout probably reflects both size selection by lampreys and a size differential in ability of fish to survive attacks. Eschmeyer (1957) believed the higher incidence of wounds on large than on small lake trout in Lake Michigan was due mainly to greater ability of large fish to survive attacks. His data showed that, during the years in which the population collapsed, abundance of lake trout shorter than 17 inches declined more rapidly than that of larger fish. Observations of the

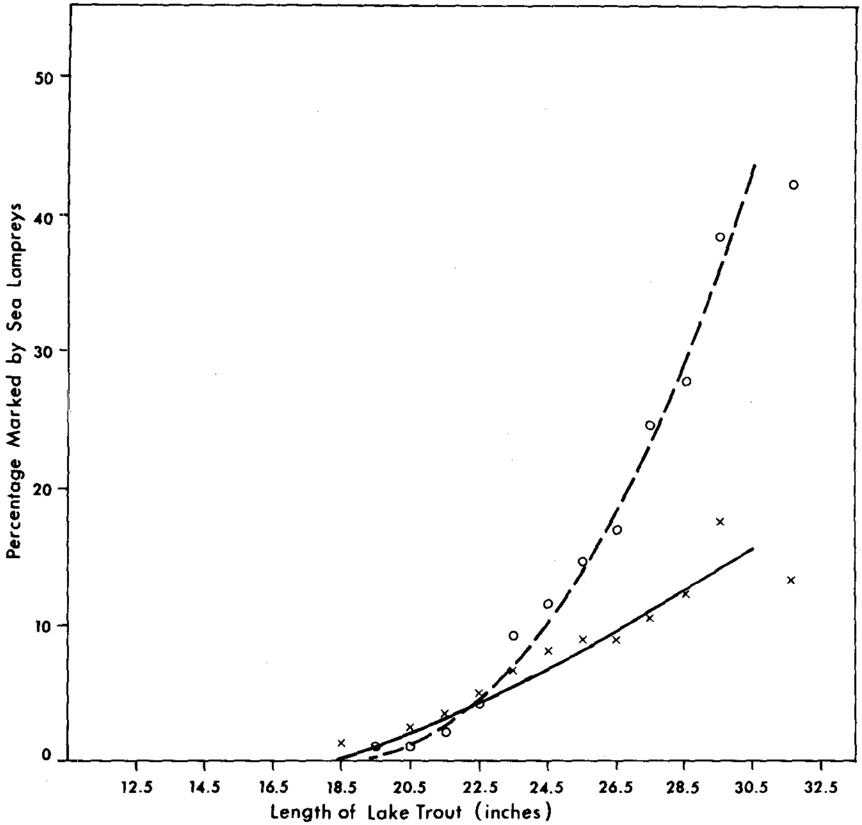

Figure 5. Percentage of lake trout of various lengths bearing sea lamprey wounds (solid line) and scars (dashed line) in Michigan waters east of the Keweenaw Peninsula, April-May 1970. (All points represent 30 or more fish. Curves fitted by inspection.)

effects of attacks during sea lamprey feeding experiments (Lennon 1954) supported Eschmeyer's belief (small fish were killed more rapidly than larger fish). Field observations of occasional large lake trout with many healed scars (as many as 13 on one large lake trout examined in 1958) also suggest that large lake trout are better able to withstand attacks than are smaller fish. Farmer and Beamish (1973) showed conclusively by a series of experiments in a 21,000-liter aquarium that sea lampreys attacked the largest individuals of four species (including lake trout) most frequently. They found that the relation between number of lamprey attacks and weight of prey could be described by a linear regression (r exceeded 0.96 for all species), "the coefficient of which is dependent on the weight range" of the prey. Lake trout used in the experiment ranged from about 0.9 to 2.4 pounds, a much smaller range than that of lake trout from Lake Superior.

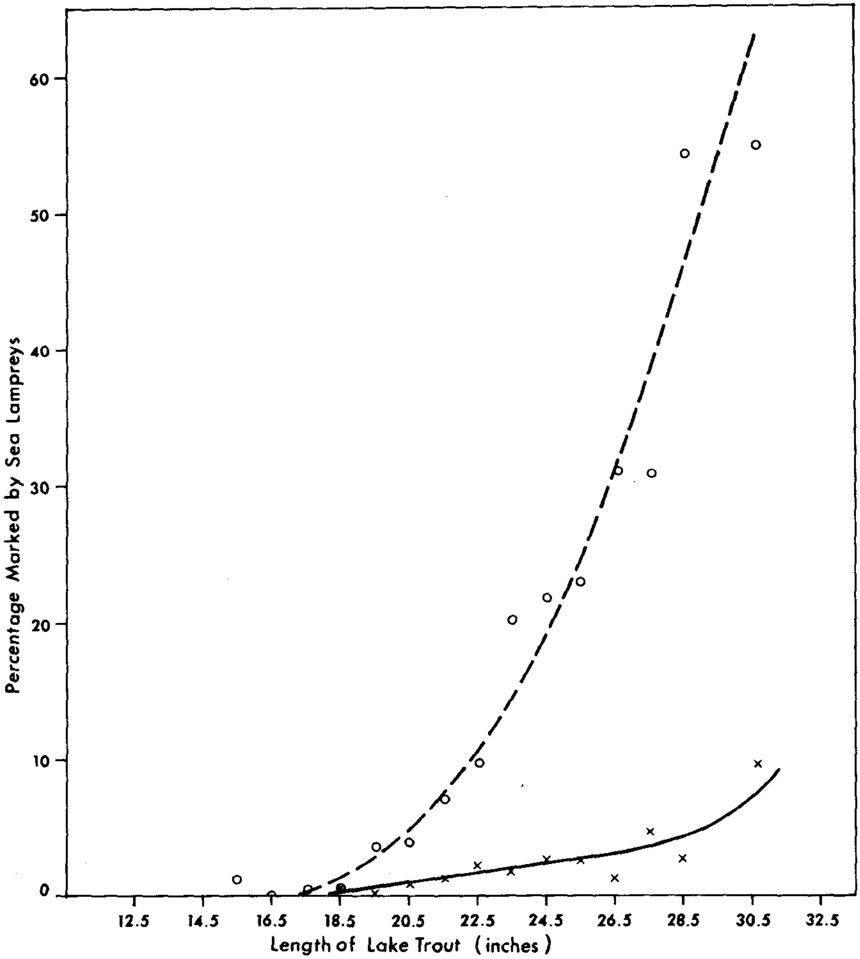

Figure 6. Percentage of lake trout of various lengths bearing sea lamprey wounds (solid line) and scars (dashed line) in Wisconsin waters, April-May 1968. (All points represent 30 or more fish. Curves fitted by inspection.)

Budd and Fry (1960) and Budd et al. (1969) showed that lake trout stocked in South Bay, Lake Huron, like the undersize fish from Lake Michigan studied by Eschmeyer, bore very few lamprey marks until after they reached a fork length of 16.5 inches at age IV but, unlike the Lake Michigan fish, suffered no higher natural mortality during the first 4 years than would be expected in waters without sea lampreys (about 20% per year). The percentage wounded or scarred each year and natural mortality increased progressively thereafter until the population disappeared at age VI or VII.

Some evidence from Lake Superior suggests that, as in South Bay, the low percentage of small lake trout with lamprey wounds was mainly a reflection of a low attack rate by sea lampreys rather than high mortality due to lamprey attacks. Pycha and King (1967) showed that the 1959 commercial

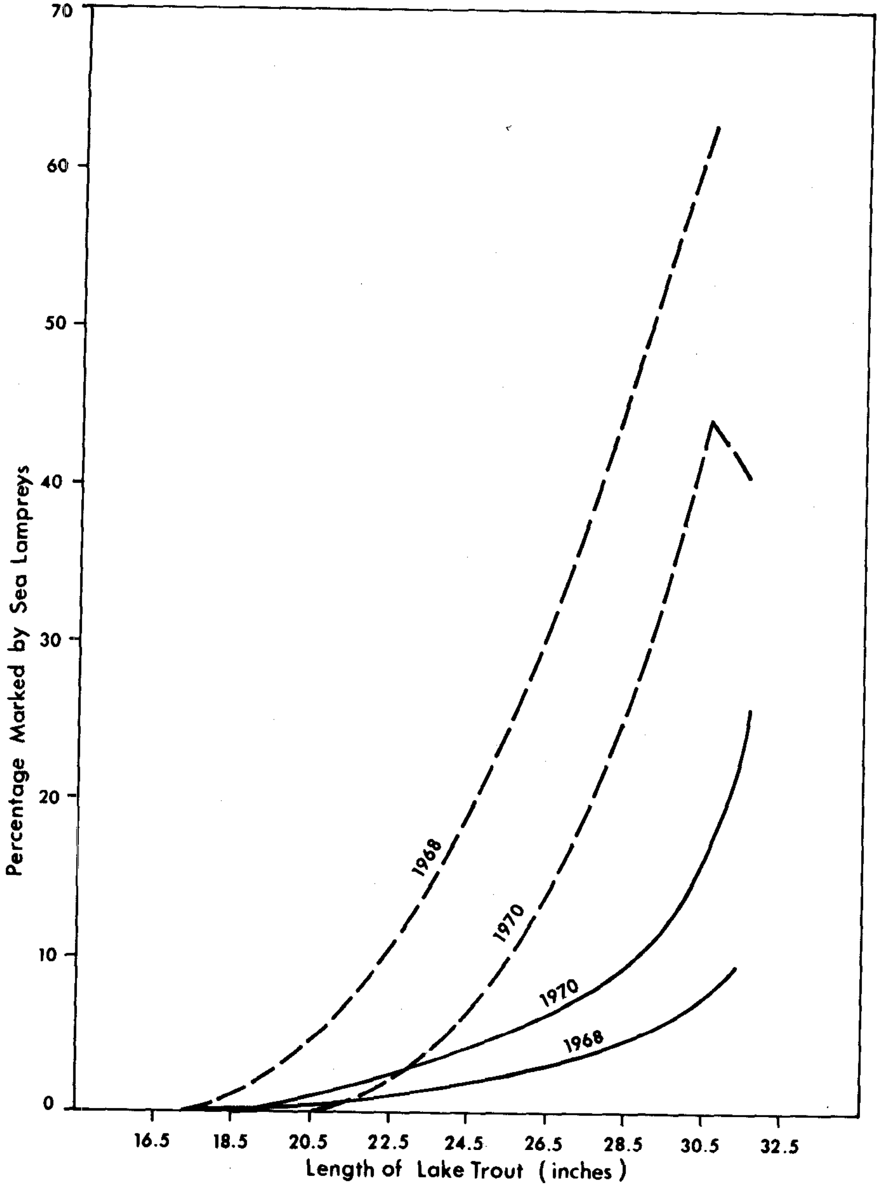

Figure 7.. Percentage of lake trout of various lengths bearing sea lamprey wounds (solid lines) and scars (dashed lines) in Wisconsin waters, April-May 1968 and 1970.

return of the lake trout planted as yearlings in Wisconsin in 1955 would not have been attained if annual natural mortality n had exceeded a constant rate of 10% at ages I-IV in 1955-58 unless fishing mortality *m* was at least 33% in 1959 (a very high figure for a year in which fishing effort was only slightly more than half that in 1952-56). Mortality of these fish was apparently not high while they were less than 17 inches long, even though sea lampreys were abundant in 1956-58 in Wisconsin waters (as indicated by the spawning runs in Wisconsin in 1957-59, Table 2).

The relations between sea lamprey wounding and scarring rates at different levels of wounding suggest that large lake trout suffer high mortality when the lamprey attack rate is high. Although we have no direct measure of attack rates and only limited information on healing rates of lamprey wounds, our criterion for wounds (open and not healed) makes it reasonable to assume that wounding rates are closely related to attack rates. If lake trout survived most lamprey attacks, high scarring would necessarily follow a high attack rate and vice versa. The relation between wounding and scarring rates, however, tends to be inverse. In 1968, when the wounding rate was low in Wisconsin waters, the scarring rate was much higher than in 1970 when wounding rates were high (Figs. 5 and 7). The differences in scarring rates in 1968 and in 1970 were not caused by differences in wounding the previous year-the general level of wounding in Wisconsin in 1967 was lower than in either Wisconsin or Michigan in 1969 (Fig. 8).

The only reasonable explanation for the inverse relation between wounding and scarring rates is that many lake trout can survive one or more lamprey attacks, but succumb to successive attacks if recovery time between attacks is short. Since sea lamprey attacks remove blood and other body fluids and also remove and damage tissue, it is reasonable to assume that attacks have a cumulative effect on the prey if the time between attacks is not long enough for complete recovery.

The greater proportional reduction in scarring with increase in wounding among small than among large fish suggests, as would be expected, that smaller fish are less able to survive successive attacks than are larger fish. The greater reduction in scarring with increase in wounding among large than among small fish, however, suggests that mortality from sea lamprey attacks is higher among large fish because of the higher attack rates on the larger fish.

Other observations indicate that, among fish longer than 17 inches, mortality from sea lamprey predation was higher among large than among small lake trout. Reduction of the sea lamprey population in mid 1961 was followed by a rapid increase in the average size of lake trout in the catch. Average dressed weight of lake trout in the Wisconsin commercial catch increased from 2.0 pounds in May 1961 to 2.8 pounds in May 1962. As is shown in a later section, this increase resulted from a sharp increase in CPE of 21.0- to 28.9-inch fish in 1962 while CPE of 17.0- to 20.9-inch fish changed little. Had the low incidence of lamprey wounds on small lake trout been mainly a reflection of extremely high mortality rather than a low attack rate, reduction of the sea lamprey population should have resulted in a greater increase in survival of small than of large lake trout and average weight would have decreased.

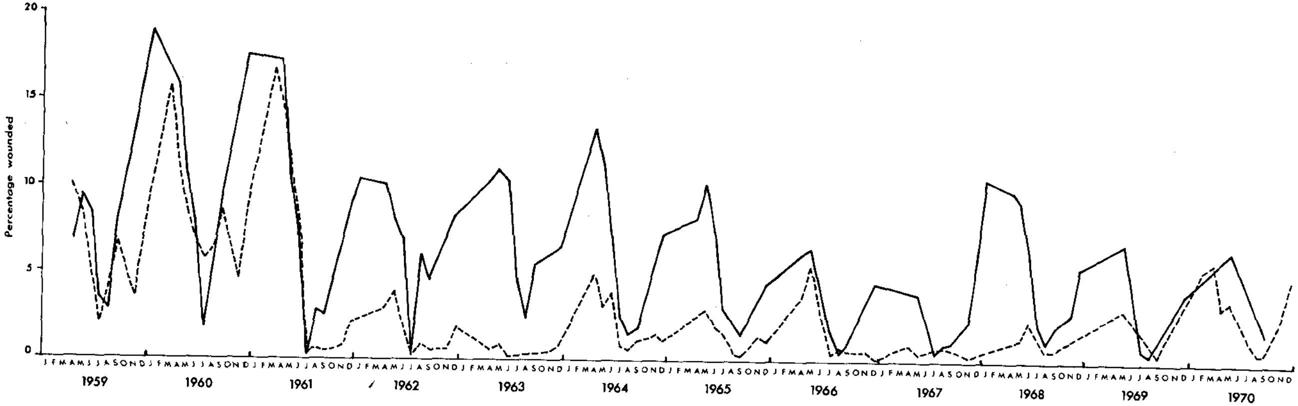

Figure 8. Percentage of legal-size lake trout (>16.9 inches, total length) bearing fresh sea lamprey wounds, by month, in Michigan waters east of the Keweenaw Peninsula (solid line), and in Wisconsin waters (dashed line), 1959-70.

Table 3. Number of lake trout of various sizes caught per 100,000 feet of 4 1/2-inch-mesh gillnet in April and May, 1948 and 1970, in Michigan waters east of the Keweenew Peninsula (data adjusted for the difference in efficiency of the cotton and nylon nets used in the two years).[a]

Length interval (inches)	Year	
	1948	1970
<17.0	187	42
17.0-20.9	392	598
21.0-24.9	384	1,923
25.0-28.9	116	959
29.0-32.9	31	55
33.0-36.9	4	1

[a] Samples came from 131,000 feet of net in 1948 and 179,000 feet in 1970.

A comparison of length distributions of lake trout from 4 1/2-inch-mesh gillnet catches in 1948 (when sea lampreys were still a rarity) and 1970 (when sea lampreys were under control but were still common) gives further evidence (Table 3), that the largest lake trout suffer higher mortality in the presence of sea lampreys than do smaller fish. In 1948, the end of a 5-year period when the fishing intensity index averaged 138, CPE of most sizes of lake trout was, as would be expected, far below that in 1970, the end of an 8-year period when the intensity index averaged only 9. CPE in 1948 was about two-thirds as high as in 1970 for 17.0- to 20.9-inch fish, about one-fifth as high for 21.0- to 24.9-inch fish, and only about one-eighth as high for 25.0- to 28.9-inch fish. CPE of fish in the 29.0- to 32.9-inch range, however, was about half as high in 1948 as in 1970, and that of 33.0- to 36.9-inch fish was higher in 1948 than in 1970. The lower CPE of 33.0- to 36.9-inch fish in the 1970 catch did not reflect lack of time for lake trout to grow to that size. The maximum length of lake trout in the spring catches increased from 29 inches in 1962 to 33 inches in 1964, but with the exception of one 37-inch fish in 1966 and one 34-inch fish in 1968, the longest fish caught each year in 1967-70 was 32 inches (2 years) or 33 inches (3 years). The greater proportion of large fish in the 1948 catch suggests that survival of fish longer than 29 inches was higher under conditions of high fishing intensity and almost no sea lampreys than under conditions of very low fishing intensity and moderate numbers of sea lampreys.

STOCKING OF LAKE TROUT

Numbers and source

Fin-clipped lake trout were stocked in Lake Superior in 19 of the 22 years from 1947 to 1968 (Table 4). Small-scale experimental planting of fin-clipped fingerlings began in Ontario in 1947; larger experimental plantings of marked fingerlings and yearlings were made in the Apostle Islands region, Wisconsin, and off Marquette, Michigan, in 1952-56. No fin-clipped fish were released in 1957, although substantial numbers of unmarked yearlings were released in Wisconsin and Whitefish Bay (Fig. 1). Annual plantings of marked

Table 4. Numbers of fin-clipped lake trout planted in the four jurisdictional areas of Lake Superior, 1947-68.

Year[a]	Minnesota		Wisconsin		Michigan		Ontario		Total	
	Fingerlings	Yearlings or older	Fingerlings	Yearlings or older	Fingerlings	Yearlings or older	Fingerlings	Yearlings or older	Fingerlings	Yearlings or older
1947							27,574		27,574	-
1948	-	-	-	-			32,469		32,469	
1950	-	-	–	-	-		49,888	-	49,888	
1952	-		145,000	102,097	65,366			-	210,366	102,097
1953	-	-	132,980	80,137	139,973	69,439	49,915		321,968	149,576
19.54			142,323	102,016	121,296	134,318			263,619	236,334
1955	–		–	102,794	-	60,744	–	-	-	163,538
1956	-			200,731	-	-	–	-	-	200,731
1958	-		-	183,964		298,148		537,870	-	1,019,982
1959	–		-	151,060	–	43,465		472,590	-	667,115
1960			49,400	161,350		393,108	50,250	395,641	99,650	950,099
1961		-	–	314,021	-	392,100	60,200	493,980	60,200	1,200,101
1962	76,559	-	-	493,168	-	775,161	-	508,175	76,559	1,776,504
1963	37,846	-		311,469	-	1,185,755	-	476,709	37,846	1,973,933
1964	–	182,000	–	743,435		1,195,770	–	472,400		2,593,605
1965		101,700	–	447,500	-	826,900	–	467,740		1,843,840
1966	151,479	107,500		376,900	-	2,217,700	-	450,000	151,479	3,152,100
1967	153,700	228,080	105,290	243,767	-	2,059,357		499,600	258,990	3,030,804
1968		223,130		239,075	-	2,260,375	-	499,740		3,222,320
Total, 1947-56	-	-	420,303	587,775	325,735	264,501	159,846[a]	-	905,884[a]	852,276
Total, 1958-68	419,584	842,410	154,690	3,665,709	-	11,647,839	110,450	5,274,445	684,724	21,430,403
Grand total	419,584	842,410	574,993	4,253,484	325,735	11,912,340	270,296[a]	5,274,445	1,590,698[a]	22,282,679

[a] No plantings in 1949, 1951, and 1957.

fish (mostly yearlings) then increased to more than 1 million in 1958-65 (1959 and 1960 excepted) and more than 3 million in 1966-68. (Because few planted lake trout enter the assessment or sport catches for at least 2 years after release, fish planted after 1968 contributed little to catches in 1969-70 and are not included in Table 4).

The intensity of stocking (number planted per unit area of water) was not uniform throughout U.S. waters. No lake trout were planted in Michigan waters west of the Keweenaw Peninsula until 1961 and none were planted in Minnesota until 1962. Numbers planted were relatively small in both areas until 1964. All stocking was done near or from the mainland shore in waters inhabited mainly by “lean” lake trout. Stocking intensity was based on the areas of water less than 40 fathoms deep because most lake trout are caught at 1040 fathoms. Stocking intensity was highest in Wisconsin in 1952-65 and in Michigan and Minnesota in 1966-68.

The origin of most of the lake trout stocked in Lake Superior can be traced to that lake. Some were from eggs obtained from hatchery brood stocks, which in turn came from eggs stripped from lake trout caught in southern Lake Superior, and others (including most of those stocked before 1958) were from eggs stripped from spawning fish caught in the lake. In the early 1960’s, a few were reared from eggs of fish caught in inland lakes of Michigan and Ontario.

Contribution to the population and fishery

The contribution of planted lake trout to the stocks available in southern Lake Superior generally increased rapidly in 1959-66 and remained high in 1967-70 (Table 5). Survival of the fish stocked in different years has varied greatly. Before the lake trout fishery was closed in 1962, returns to the commercial fishery from various releases ranged from 1 to 37% (Pycha and King 1967). Plantings in Wisconsin generally yielded greater returns than those in Michigan, but Dryer and King (1968) reported that survival during the first year after release of fish planted in Wisconsin declined after 1961. Dispersal of lake trout from planting sites was not random, but tended to follow the counterclockwise currents in the lake (Pycha et al. 1965). Lake trout planted in Wisconsin thus made a strong contribution to stocks in Michigan waters west of the Keweenaw Peninsula and a small contribution to those in waters east of the peninsula; few fish moved in the opposite direction.

The experimental plantings made before 1957 added little to stocks of legal-size lake trout, except in western Lake Superior where, in 1959, more than 35% of the legal commercial catch in Wisconsin and 11.5% of that in Michigan waters west of the Keweenaw Peninsula were of hatchery origin (Table 5). A major portion of the catch of marked fish in 1959 was from the extraordinarily successful 1955 Wisconsin planting (Pycha and King 1967). The percentages of fin-clipped fish in the catches declined in 1959-61 in Wisconsin and in 1960-61 in western Michigan as fish of the 195 5 planting disappeared.

The contribution of planted lake trout to the legal-size stocks increased again after 1961 as a result of the increasing annual plantings in 1958-64. In Wisconsin, the percentage of fin-clipped fish increased rapidly in 1962-66, reached a peak of 96% in 1968, and declined slightly to 90% in 1970. In

Table 5. Percentage of undersize and legal lake trout with clipped fins landed by commercial assessment fishermen from inshore waters of Lake Superior, 1959-70 (numbers of fish in parentheses).[a]

Year	Wisconsin		Michigan			
			West of Keweenaw		East of Keweenaw	
	Undersized	Legal	Undersized	Legal	Undersized	Legal
1959	24.6 (1,647)	35.3 (9,013)	32.0 (823)	11.5 (3,441)	 (7,571)	1.2 (92,484)
1960	27.8 (1.154)	28.8 (7,597)	5.1 (314)	18.3 (1,780)	8.3 (4,739)	1.5 (45,878)
1961	51.2 (934)	21.1 (9,376)	30.5 (269)	16.1 (2,783)	23.2 (3,229)	8.5 (24,215)
1962	66.1 (705)	32.8 (8.478)	57.3 (103)	22.7 (1,274)	83.4 (1,382)	27.1 (11,718)
1963	90.5 (1,134)	53.5 (13,155)	79.4 (112)	29.7 (1,399)	90.7 (2,430)	40.3 (14,883)
1964	95.7 (1,277)	69.7 (14,580)	93.6 (549)	47.7 (1,572)	91.2 (3,443)	70.6 (15,319)
1965	97.3 (1,079)	83.5 (19,277)	95.9 (446)	72.4 (1,306)	98.7 (3,420)	88.8 (14,811)
1966	97.9 (1,073)	89.7 (17,537)	97.6 (337)	91.5 (1,905)	91.9 (2,828)	95.4 (15,118)
1967	92.8 (2,264)	93.1 (17,012)	97.3 (295)	96.4 (1,046)	98.5 (801)	98.5 (15,596)
1968	91.0 (2,666)	95.6 (14,007)	95.4 (108)	97.3 (1,097)	96.9 (519)	99.5 (16,888)
1969	85.0 (688)	94.3 (5,923)	92.5 (67)	97.6 (1,065)	98.1 (577)	99.3 (19,444)
1970	82.6 (944)	89.8 (15,784)	93.5 (46)	98.1 (1,058)	96.3 (297)	98.4 (11,377)

[a] Minimum legal size is assumed to have been 17 inches in all areas in all years even though the Michigan limit was based on weight in 1959-67 (see text).

western Michigan, the percentage increased rapidly in 1962-66 and continued gradually upward to 98% in 1970.

The percentage of fin-clipped fish in the undersize portion of the Wisconsin catch increased steadily in 1959-66 to a high of 98%. Natural reproduction in Wisconsin in 1965-66 (described by Dryer and King 1968) and reduced stocking in 1967-68 combined to reduce the percentage to 83% in 1970. In western Michigan waters the contribution of planted fish to stocks of undersize lake trout reached a peak of 98% in 1966, but declined slightly to 94% in 1970. This slight decline could have been due to migration of juvenile native fish from Wisconsin waters rather than to natural reproduction locally.

Hatchery fish made up only 1.2 to 1.5% of the legal-size catch in Michigan waters east of the Keweenaw Peninsula in 1959-60, but the percentage then rose steadily to 99.5% in 1968 and remained very high through 1970-perhaps 100%, since some clipped fins regenerate and occasional fish are missed during the fin-clipping process.

Hatchery fish made up a rapidly increasing proportion of the catch of undersize lake trout in eastern Michigan waters, from only 3% in 1959 to 99% in 1965; the percentage fluctuated slightly, but remained above 96% in 1966-70 (Table 5). The small fluctuations in percentages in 1966-70 and the difference between the peak percentages for undersize and legal-size fish may have resulted from occasional catches of small native siscowets, many of which are difficult to distinguish from lean lake trout until they attain a length of 12 to 16 inches.

Most of the lake trout stocks along the south shore of Lake Superior were of hatchery origin in 1964-70. Although native lake trout made up a steadily increasing proportion of the undersize fish in Wisconsin in 1967-70, much of that increase was directly attributable to the reduction in the numbers of fish planted after 1964 (Table 4). Recruitment remained strongly dependent on stocking. In Michigan inshore waters, the stocks of lean lake trout were composed almost entirely of hatchery fish through 1970.

CHANGES IN SIZE COMPOSITION AND ABUNDANCE OF LAKE TROUT, 1959-70

Lake trout taken in commercial or assessment catches were grouped by length to illustrate changes in important size segments of the population (Table 6). Since the data originated from catches in 4 1/2-inch-mesh gillnets, catch rates of the various size groups reflect to some degree selectivity of the nets as well as abundance of the various sizes of lake trout. Selectivity of the 4 1/2-inch nets has not been accurately determined for all sizes of lake trout, but recently available data (unpublished) from experimental fishing enable us to give an approximate description, Selectivity is not as sharply defined for lake trout as for many species due to a propensity of lake trout to become entangled in the nets by their teeth or mouth parts. Efficiency of the nets is low for lake trout less than 17 inches long, and increases rapidly with length of fish between 17 and 20 inches. The 4 1/2-inch nets appear to have about the same efficiency for all lengths of trout in the 20- to 30-inch range. Efficiency then falls off rapidly for 31-inch and larger fish. Out data permit only rough estimates of efficiency for fish outside the 20- to 30-inch length range. The nets appear to be about half as efficient for fish 18.5 inches long and about one-third to one-fourth as efficient for 33-inch fish as for those 20 to 30 inches long.

Among the length groups in Table 6, undersize lake trout (less than 17 inches long) seldom made up a large part of the catch. Because the proportion of undersize fish returned to the water depended on the length of time the gear was fished and on the individual fisherman's methods and handling of the fish, the catch rates for undersize fish are not dependably comparable in all years. No detectable changes in fishing practices occurred in 1959-63, but in 1964-70 the reduction in the time the nets were fished and other more subtle changes increased the proportion of undersize fish returned alive to the water and biased the data. Lake trout in the "17- to 20-inch group" (i.e., fish 17-O-20.9 inches long) made up most of the annual recruitment. Fish in this length range had a relatively low incidence of sea lamprey wounds and those shorter than 20 inches were not fully vulnerable to the commercial gillnets. Fish in the 21- to 24-inch group had moderately high lamprey wounding rates and were fully vulnerable to the fishing gear. Lake trout 25-28 inches long had much higher lamprey

Table 6. Numbers of lake trout of various sizes caught per 100,000 feet of 4 1/2-inch mesh gillnet in April and May, 1959-70 in Wisconsin waters and Michigan waters east of the Keweenaw Peninsula. [a]

Area and length interval (inches)	Year 1959	1960	1961	1962	1963	1964	1965	1966	1967	1968[b]	1969[c]	1970
Wisconsin												
< 17.0	54	61	47	44		61	50	46	43	-	-	62
17.0-20.9	191	184	273	275	454	492	542	410	523	-	-	1,039
21.0-24.9	149	55	73	460	297	476	592	781	1,027	-	-	1,826
25.0-28.9	24	5	2	36	53	127	185	274	298	-	-	746
> 28.9		0	0	0	1	11	23	32	36	-		64
Total legal	3662	244	348	771	805	1,106	1,342	1,497	1.881	-	-	3,675
Michigan												
< 17.0	65	56	51	16	66	73	97	112	39	19	43	
17.0-20.9	497	334	326	152	191	167	292	397	660	953	611	598
21.0-24.9	286	197	118	218	224	185	179	288	442	1,340	1,513	1,923
25.0-28.9	17	10	5	20	45	68	66	55	54	147	359	959
> 28.9	0	0		0	3	7	10	9	4	5	7	56
Total legal	800	541	449	390	463	427	547	749	1,160	2,445	2,490	3,535

[a] The amount of gillnet lifted in Wisconsin ranged from 110,000 feet in 1967 to 675,000 feet in 1959; in Michigan the range was from 179,000 feet in 1970 to 4,586,000 feet in 1959.

[b] No assessment fishing in the spring of 1968 in Wisconsin.

[c] The size distribution of the 1969 catch in Wisconsin was not comparable with that in other years because fishing was begun later in the year than usual.

wounding rates than the smaller fish and were also fully vulnerable to the gear. Since the smallest mature females were about 25 inches long (Eschmeyer 1955), this group partially reflected abundance of spawning stocks. Fish longer than 28.9 inches (very few were longer than 33 inches in 1959-70) generally had the highest incidence of lamprey wounds, but the few largest fish in the group frequently had lower wounding rates than smaller fish, and commonly bore no wounds. The larger fish within this size group were less than fully vulnerable to the fishing gear. Lake trout longer than 28.9 inches made up the bulk of the spawning stocks before the mid 1950's (Eschmeyer 1955).

Year-to-year comparisons of relative abundance of lake trout within any given size group of Table 6 are not invalidated by net selectivity. Direct comparisons between size groups, whether within or between years, are valid only for the 21- to 24-inch and the 25- to 28-inch groups. Although direct comparisons of abundance of lake trout in groups outside the 21- to 28-inch range with that of fish in this range are biased by net selectivity, changes in the proportions of the catch falling within the various size groups reflect changes in growth rate, survival rate, or rate of recruitment. Average growth increments of lake trout 17-30 inches long caught in the mid 1960's were generally close to the 3- to 4-inch average of the early 1950's found by Rahrer (1967). Growth rate declined slightly in the late 1960's but the decline was gradual. Year-to-year changes in the catch rates of the various size groups, therefore, reflect mainly changes in rates of recruitment and survival.

In 1959-61, abundance of all sizes of lake trout declined in Michigan waters and all sizes 21 inches and longer declined in Wisconsin waters (Table 6). Spawning stocks were very low in both states in 1959 and, by 1960, fish 25-28 inches long were scarce and those longer than 28.9 inches were almost gone. Although vulnerability of fish less than 17 inches was low and 17- to 20-inch fish were incompletely vulnerable, the declines in these groups in Michigan were real and reflected declining recruitment. The 1961 increase in the 17- to 20-inch group in Wisconsin was also real and was caused either by unusual strength of the 1956 year class of native lake trout or by exceptionally high survival of the unclipped lake trout of the same year class planted in 1957.

In 1962, abundance of 21- to 24-inch and 25- to 28-inch fish increased sharply in both Wisconsin and Michigan. These increases reflected sharp increases in survival rate. Most growth of lake trout in Lake Superior occurs after midsummer (Rahrer 1967); the increases in abundance were almost entirely due to reduced mortality of the fish that advanced to larger size groups during the fall and early winter of 1961. In Wisconsin, abundance of undersize fish declined slightly and that of 17- to 20-inch fish held at the 1961 level. In Michigan, abundance of 17- to 28-inch fish declined even more rapidly than in 1959-61 and fish less than 17 inches long became scarce. Of the few undersize fish caught in Michigan in 1962, 83% were fin-clipped (Table 5).

In Wisconsin, recruitment was much higher in 1963-70 than in 1959-62. Abundance of 17- to 20-inch fish increased sharply in 1963 and rose to nearly four times the 1961-62 level by 1970. The catch rate of undersize fish also increased in 1963 but the data for undersize fish after 1963 are not reliable and are almost certainly underestimates. Except for the 21- to 24-inch group in 1963, abundance of all sizes of lake trout 21 inches long and longer increased steadily after 1962. By 1964, abundance of 25-inch and larger fish had increased to 3.5 times that in 1959 and a substantial spawning run was reestablished on one major spawning ground. In 1965, native young-of-the-year lake trout were taken in experimental trawls by the Service's research vessel *Siscowet* for the first time in 6 years (Dryer and King 1968).

The proportion of the Wisconsin catch made up of 21-inch and larger lake trout declined somewhat in 1963, but increased more than threefold in 1963-67. This increase can be accounted for only by a substantial increase in survival rate, but increased-survival was confined mainly to fish less than 25 inches long. The increase in abundance of 25-inch and larger fish in 1963-67 was therefore due mainly to growth of the increasing numbers of fish in the 21- to 24-inch group while survival rate of 25-inch and larger fish apparently changed little. Lack of data for 1968-69 prevents evaluation of changes in survival in 1967-70, but the high abundance of 17- to 20-inch and 21- to 24-inch fish in 1970 suggests that increasing recruitment rather than any major change in survival accounted for most of the continued increase in abundance of fish 25 inches long and longer.

The changes in abundance of the various size groups in Michigan waters in 1963-70 were similar to those in Wisconsin, except that recruitment into the 17- to 20-inch group declined through 1964 and was relatively low until 1967. Low abundance of 17- to 20-inch fish in 1962-64 caused low recruitment into the 21- to 24-inch group in 1963-65. A steady increase in recruitment of 17- to 20-inch fish in 1965-68 was followed by a greater than proportional increase in the 21- to 24-inch group in 1966-70. The increase of 21- to 24-inch fish in Michigan, as in Wisconsin, indicates that survival as well as recruitment was increasing. Lake trout 25 inches long and longer increased approximately in proportion to the abundance of 21- to 24-inch fish a year earlier in 1963-69, but in 1970 abundance of 25- to 28-inch fish almost trebled and that of fish longer than 28.9 inches increased eightfold. This sharp increase of 25-inch and larger fish could have occurred only if survival of these large fish increased substantially.

CAUSES OF THE CHANGES IN THE LAKE TROUT POPULATION

The available information on changes in fishing effort and on abundance of lake trout in the late 1940's and early 1950's strongly favors the belief that intensive fishing, aided by the introduction of nylon gillnets, was the principal factor involved in the early years of the post-World War II decline of lake trout in Lake Superior. The point at which sea lamprey predation became a serious source of lake trout mortality is not known, but it was probably sometime in the early to mid 1950's in Michigan waters of the lake. Smith (1968) showed that the intensively fished lake trout stocks of lakes Huron and Michigan began to decline within a few years after the sea lamprey was first recorded in each of those lakes and long before the lampreys reached their peak abundance. Irrespective of the relative importance of the fishery and sea lamprey predation in the early and mid 1950's, together they caused a serious depletion of the stocks-most importantly those of large spawning-size fish. Reports of many commercial fishermen indicated that spawning stocks were drastically depleted by 1956 or 1957 in Michigan waters and by 1957 or

1958 in Wisconsin waters. By the end of the 1950's natural reproduction ranged from poor to almost nonexistent, and by the mid 1960's, the recruitment of legal-size native fish was severely curtailed.

In 1959-61, the population of native lake trout fell rapidly, due both to declining recruitment and high mortality of legal-size fish. Even though fishing effort had been reduced greatly during the late 1950's, total mortality remained so high that all previous accumulations of spawning stocks were gone by 1960 and almost no female lake trout survived to maturity in 1960 or 1961. The sharp increases in survival and abundance that occurred in the fall of 1961 and in 1962, immediately after the reduction in abundance of sea lampreys, while the commercial fishery was still open and the contribution of planted lake trout was still minor, clearly indicated that sea lampreys had become a greater source of mortality than the fishery by the 1960's.

In 1962-70, abundance of lake trout was dependent mainly on the intensity of stocking 3 to 7 years earlier and on the mortality rate of legal-size fish. The intensive and Increasing rate of stocking in Wisconsin during the 1950's slowed the decline in recruitment in 1959-60 and reversed the decline there in 1961. Recruitment increased slightly in 1961 and 1962 and sharply in 1963, and was maintained at a high level throughout the remainder of the 1960's. Although the natural reproduction of the mid 1960's made an increasing contribution to the total catch of undersize and legal fish in the late 1960's, almost 90% of the legal-size catch was still made up of stocked fish in 1970. In Michigan, stocking rates were much lower than in Wisconsin in the 1950's and were not increased substantially until 1960. The decline in recruitment was not reversed there until 1965, by which time almost all small native lake trout were gone (99% of the undersize fish were fin-clipped). Recruitment then increased rapidly in 1965-68. In both Wisconsin and Michigan, recruitment of stocked fish was high enough during the middle and late 1960's to increase the abundance of legal-size fish rapidly through 1970.

Although the mid 1961 reduction of sea lamprey abundance resulted In immediate reduction of sea lamprey wounding rates and in clearly discernible increases in survival of lake trout, recovery of spawning stocks was limited through 1970. The available evidence indicates that increase in the average age and size of spawners was restricted by high mortality. Even in Wisconsin, where some natural reproduction was reestablished by the fall of 1964 (minimum age for maturity of females was VII), relatively few fish survived past age IX in 1965-70. Age IX was probably the youngest age at which all or nearly all females were mature, on the basis of the studies of Eschmeyer (1955) and Dryer and King (1968) and our subsequent unpublished data from Gull Island Shoal, Wisconsin.

Relative abundance data from several successive year classes in the 1965-69 spawning runs at Gull Island Shoal indicated that total annual mortality from age IX to age X was about 0.75. The tagging study of Rahrer (1968) and subsequent tagging and returns from this population (unpublished) indicated that the rate of exploitation by commercial and sport fishing combined was no greater than 0.10 in 1965-70. The instantaneous rate of natural mortality, M, derived from the figures above is 1.21. This value of M for age IX-X fish in the late 1960's is much higher than the value Sakagawa and Pycha (1971) found for total mortality of lake trout of the same ages in

1948 (Z = .70) when the commercial fishery was operating at far above normal intensity and the sea lamprey was still rare in Lake Superior. This high natural mortality accounts for the scarcity of fish over 33 inches long in the commercial catches mentioned earlier.

The cause of the high natural mortality has not been positively determined. Circumstantial evidence, however, suggests strongly that sea lamprey predation is a major cause of the mortality of large lake trout. The incidence of fresh lamprey wounds on lake trout taken during the spawning run on Gull Island Shoal was not high in 1965-70, but the incidence of wounded fish in the October spawning run perhaps does not reflect the true extent of sea lamprey predation. Lamprey wounding rates were invariably highest in the spring (Fig. 8). In addition, wounding rates on large lake trout caught in late September within a few miles of Gull Island Shoal were much higher than on the same sizes of fish caught on the spawning reef in mid October. The low incidence of both fresh and partially healed wounds on spawning lake trout suggests that a lamprey attack and the resulting wound inhibit the urge or capacity to spawn, and that feeding adult sea lampreys are rare or absent on the shallow shoals used by spawning lake trout.

High rates of attack in the late 1960's were apparent, however, from the incidence of healed scars. In 1969, for example, 5% of 160 spawners 25.0-28.9 inches long, 83% of 149 fish 29.0-32.9 inches long, and all 26 fish 33 inches and longer bore healed scars. Fish in the smallest of these size groups bore an average of 0.7 scar per fish and those in the largest group averaged 4.2 scars per fish. Back-calculated annual growth increments of individual 8- to 10-year-old fish caught in 1970 ranged from 1.3 to 4.0 inches and averaged 2.5 inches. The time required for lake trout to grow from 27 inches (the midpoint of the 25.0- to 28.9-inch interval) to well over 33 inches was, therefore, 2-4 years. During that time, the average number of scars per fish increased sixfold and the fish over 33 inches long had survived an average of 3.5 attacks per fish. Although the evidence is clear that some large lake trout can survive several lamprey attacks, the inverse relation between wounding and. scarring rates illustrated in an earlier section is evidence that many lake trout must also have succumbed.

Unlike most lake trout in southern Lake Superior, most of the Gull Island Shoal spawners were native rather than stocked fish. Their growth rate in the late 1960's was somewhat slower at ages VIII-X than that reported by Rahrer (1967) for lake trout in eastern Lake Superior in 1953. High mortality and short life span often associated with unusually fast growth should not apply to this group.

Mortality at ages below IX has not been determined for the Gull Island Shoal fish. Total mortality determinations on several groups of stocked lake trout in Michigan waters, however, indicated that total mortality of fully vulnerable fish (20 inches and longer) increased with age and size in a manner similar to the increase in sea lamprey wounding with size. Total mortality at age IX was as high as or higher than that for the Gull Island Shoal spawners. As with the Gull Island Shoal fish, no other major cause of mortality was apparent.. Rate of exploitation from the assessment and sport fisheries combined, estimated from tag returns, was only about 0.10. Changes in the fishery in prior years could not account for the inordinately high mortality of the older, larger fish. Assessment fishing intensity declined during the late 1960's and sport fishing increased. Although the sport catch was estimated to be several times as large as the assessment catch by 1970 (Asa T. Wright, personal communication), field observations and tag returns indicated that the size composition of the sport and assessment catches was similar. The total estimated catch from sport and assessment fishing increased almost directly in proportion to the relative abundance of legal-sized fish. Fishing mortality rate, therefore, probably changed little in 1965-70; only the apportionment among users changed.

Spawning stocks were limited both by increasing mortality with size among the larger immature fish, which reduced recruitment of spawners, and by very high mortality within the spawning stocks. Fishing mortality accounted for only a small part of the total mortality, and natural mortality appeared to be nearly as high on the native stocks of Gull Island Shoal as on stocks of planted fish. Differences in mortality and maximum size of fish in the assessment catches were generally associated with sea lamprey wounding rates. Although the evidence linking sea lamprey wounding to this high mortality is largely circumstantial, the consistency of the relation between lamprey wounding rates and mortality, the inverse relation between lamprey wounding and scarring rates, and the lack of evidence of any other source of high mortality of lake trout leads us to conclude that sea lamprey predation was a major factor and probably the principal factor limiting abundance and size of lake trout spawners in 1962-70.

The progressive increase in survival of 21- to 24-inch lake trout in the middle and late 1960's was probably a result of reduction of sea lamprey predation on fish of that size. Abundance of legal-size lake trout almost tripled in Wisconsin and increased sixfold in Michigan (Table 6) while abundance of sea lampreys declined somewhat in 1965-70 (Table 2). The resultant reduction of the predator-prey ratio and the preference of sea lampreys for larger prey resulted in an upward shift in the size of lake trout attacked by lampreys and lower mortality of the small legal-size fish. Since fishing mortality appears to have changed little in 1965-70, this increase in survival was probably unrelated to fishing.

The relative importance of the various factors that affected the abundance and size composition of lake trout can, at present, be only qualitatively estimated. The combination of limitations on fishing effort, sea lamprey control, and stocking, however, clearly resulted in roughly a tenfold increase in numerical abundance of legal-size fish and in a substantial increase in the average size of lake trout in 1961-70. Insufficient natural reproduction to sustain the population was the main weakness in an otherwise strong recovery of the population. We believe that predation by sea lampreys was a major factor limiting abundance and size of mature lake trout in the late 1960's. Further reduction of sea lamprey abundance should increase abundance of lake trout spawning stocks. Since the population was composed mainly of hatchery-reared fish by 1970, other unknown or ill-defined problems induced by hatchery rearing or stocking could also have affected the population.

Recent observations, for instance, indicate that relatively few lake trout that were stocked along the mainland shore used the native lake trout spawning grounds, most of which were a considerable distance from shore. Many, however, attempted to spawn in nearshore areas not formerly used as spawning grounds. These observations suggest that planted lake trout home to planting sites or similar onshore areas-many of which are probably unsuitable for incubation of eggs or survival of fry. Stocking on or in proximity to former spawning grounds may be necessary to increase reproductive success of hatchery-reared lake trout. Continued heavy stocking to maintain recruitment, and limitations on total catch to control fishing mortality will be necessary to maintain an acceptable predator-prey ratio until natural reproduction has increased substantially.

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