LAKE MICHIGAN

Man's Effects on Native Fish Stocks and Other Biota

Great Lakes Fishery Commission

TECHNICAL REPORT No. 20

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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Man's Effects on Native Fish Stocks and Other Biota

by

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GREAT LAKES FISHERY COMMISSION
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FOREWORD

This paper is one of seven lake case histories-Lake Superior, Lake Michigan, Lake Huron, Lake Erie, Lake Ontario, Lake Opeongo, and Lake Kootenay. Concise versions of these papers, together with other lake case histories developed for and by an international symposium on Salmonid Communities in Oligotrophic Lakes (SCOL) appeared in a special issue of the Journal of the Fisheries Research Board of Canada (Vol. 29, No. 6, June, 1972).

While this and each of the others in this series is complete in itself, it should be remembered that each formed a part of SCOL and is supplemented by the others. Because much detail of interest to fisheries workers in the Great Lakes area would not otherwise be available, this and the other case histories revised and refined in the light of events at the symposium are published here.

SCOL symposium was a major exercise in the synthesis of existing knowledge. The objective was to attempt to identify the separate and joint effects of three major stresses imposed by man: cultural eutrophication, exploitation, and species introduction on fish communities. Recently glaciated oligotrophic lakes were chosen as an "experimental set." Within the set were lakes which have been free of stresses, lakes which have been subjected to one stress, and lakes which have been subjected to various combinations of stresses. The case histories provide a summary of information available for each lake and describe the sequence of events through time in the fish community. Some of these events were inferred to be responses to the stresses imposed. Lakes Opeongo and Kootenay were included in this set somewhat arbitrarily, with the case histories of the Laurentian Great Lakes, to illustrate similarities and differences in the problems associated with other recently glaciated oligotrophic lakes.

We began organizing SCOL in 1968 and were later supported by a steering committee: W. L. Hartman of the U.S.A., L. Johnson of Canada, N.-A. Nilsson of Sweden, and W. Nümann of West Germany. After two years of preparation, a work party consisting of approximately 25 contributors and a similar number of interested ecologists convened for two weeks in July, 1971 at Geneva Park, Ontario, Canada.

Financial support was provided by the Great Lakes Fishery Commission, Ontario Ministry of Natural Resources, Fisheries Research Board of Canada, Canadian National Sportsman's Show, and University of Toronto.

Editorial assistance was provided by P. H. Eschmeyer, K. H. Loftus, and H. A. Regier.

K. H. Loftus
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Man's Effects on Native Fish Stocks and Other Biota[1]

by

LaRue Wells and Alberton L. McLain

ABSTRACT

Man's activities have caused great changes in Lake Michigan in the past 120 years. Although changes in water chemistry and lower biota have been generally modest (except locally), those in native fish stocks have been vast. Exploitation, exotic fish species, and eutrophication and other forms of pollution all have played a role in bringing about the changes (mostly declines in abundance) in fish populations.

Exploitation resulted in a noticeable reduction in abundance of certain native species (especially whitefish) soon after the establishment of the commercial fishery in the 1840's. By the 1930's the sturgeon and the two largest deepwater ciscoes (Coregonus *nigripinnis* and C. *johannae)* became severely depleted. Other species-whitefish *(Coregonus clupeaformis),* lake trout *(Salvelinus namaycush),* and lake herring (C. artedii)-remained important commercially, but at a lower level of production than originally; greatly increased fishing effort and efficiency were required to maintain even these decreased catches. The catch of intermediate-size ciscoes held relatively stable, but again only through sharply increased fishing effort and efficiency.

The earliest serious effects of exotic fish species on native fish stocks may have been during the *1930's,* when smelt *(Osmerus mordax)* first became abundant. Powerful influences by exotics were not obvious, however, until the 1940's, when the sea lamprey's *(Petromyzon marinus)* predation on several species, particularly the lake trout, became critical. In the 1950's the sea lamprey was joined by the alewife *(Alosa pseudoharengus),* another exotic strongly deleterious to several native fish. The alewife apparently inhibited reproduction of deepwater ciscoes, yellow perch *(Perca flavescens),* deepwater sculpins *(Myoxocephalus quadricornis),* emerald shiners *(Notropis atherinoides),* and perhaps others (through competing with young, or feeding on them). At the same time, however, the alewife as a prolific forage fish has made possible the highly successful introduction of several species of salmonines.

The effects of accelerated eutrophication and other pollution, although not always as easy to identify as the influences of other factors, were-nevertheless clearly important as early as the mid-1800's. The first conspicuous contamination of Lake Michigan was by sawmill wastes, which covered spawning-grounds in streams and around stream mouths. This type of pollution was particularly destructive to whitefish. Other forms of stream degradation (e.g., dams, deforestation of watersheds) although not strictly "pollution," must also have been detrimental to stream spawners. Heavy pollution in southern Green Bay (a large area of the bottom of which is now covered with anoxic gray sludge) probably has resulted in reduction in abundance of several species, e.g., lake herring and *walleye (Stizostedion v. vitreum).*

Exploitation was largely responsible for the changes in Lake Michigan fish stocks before the invasion of the smelt, and probably before the invasion of the sea lamprey.

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1 Contribution 462, Great Lakes Fishery Laboratory, U.S. Fish and Wildlife Service, Ann Arbor, Michigan.

The lamprey and alewife, however, have exerted a greater impact than the fishery on native fish populations in recent decades. Accelerated eutrophication and other pollution, although important, have not equalled the other factors in causing changes in native fish populations.

INTRODUCTION

Lake Michigan, the world's sixth largest lake in both area and volume, is the only one of the Laurentian Great Lakes that lies entirely within the boundaries of the United States. It is divided among four political subdivisions-the states of Michigan, Wisconsin, Illinois, and Indiana-each with complete jurisdiction over the waters within its borders. By far the greatest shares belong to Michigan and Wisconsin.

The first rapid population growth around Lake Michigan began early in 1832, when termination of Indian hostility in Illinois encouraged settlement along the southwestern shore. In 1832 alone, the population of Chicago increased from 150 to an estimated 2,000 (Hatcher 1944). Settlements thereafter sprang up quickly at the major river mouths and harbors along shore.

The influx of settlers soon caused significant changes in the Lake Michigan environment, due largely to rapidly developing commercial fishing and lumbering operations. By 1850 fishing was a major industry. Changes in certain fish stocks, probably mostly due to heavy exploitation, were noticed by the late 1850's. By that time, however, pollution of rivers and their estuaries from sawmills and other sources, and other alteration of streams (e.g., deforestation, drainage, and construction of dams) had also begun to affect fish stocks. In the mid-1900's the introduction of several exotic fish species (indirectly as a result of man's activities) had devastating effects on the native fish stocks.

Changes in fish stocks have continued to the present. Other environmental changes may also have occurred more or less constantly since the early days of settlement, but data for making comparisons are almost non-existent. Limited comparative data for recent decades have shown changes in water chemistry and lower biota, but generally these changes have been much less obvious than those in the fish stocks.

Beeton (1969) reviewed changes in Lake Michigan, primarily with respect to eutrophication, and Smith (1968, 1970) described certain aspects of changes in the fish stocks and discussed reasons for these changes. The primary purpose of the present report is to describe further the changes brought about by exploitation, exotic fish species, and accelerated eutrophication and other forms of pollution on the environment of Lake Michigan, with particular reference to their effects on native fish stocks.

DESCRIPTION OF LAKE MICHIGAN

Lake Michigan is in the north central United States, and lies between 41°37′ and 46°06′ North Latitude, and between 84°45′ and 88°02′ West Longitude (Fig. 1). Its length is 307 miles (494 km), its maximum width 118

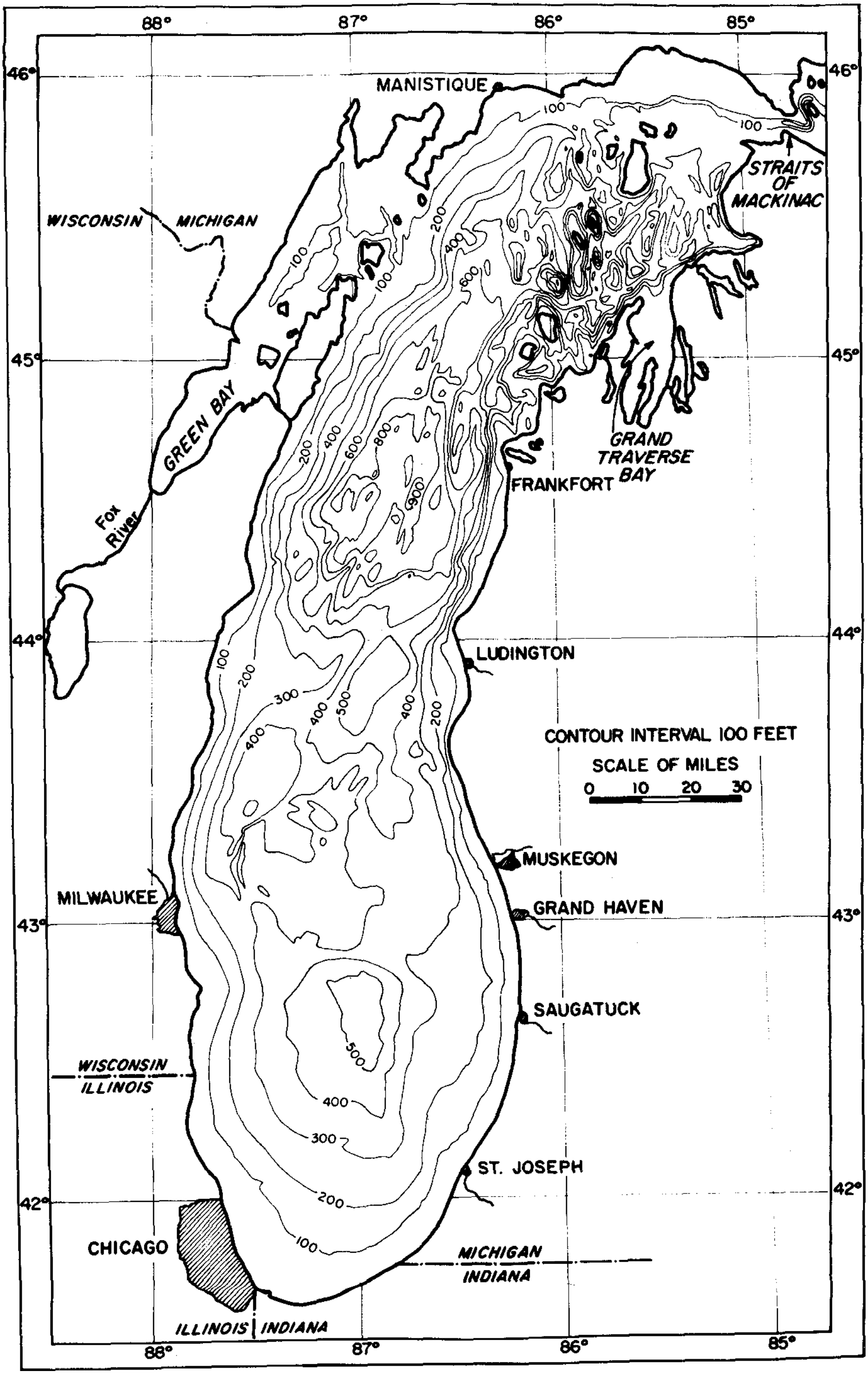

Figure 1. Lake Michigan (modified from Hough 1958). Grand Traverse Bay, which is not contoured, has a steeply sloping bottom and a maximum depth of about 600 feet.

miles (190 km), its shoreline length 1,661 miles (2,672 km), and its surface area 22,400 square miles (58,200 km^2). The mean depth is 276 feet (84 m) and volume of water 1,170 cubic miles (4,870 km^3). The drainage basin, including the lake, covers 67,860 square miles (175,760 km^2). No tributary stream has an average flow greater than 3,400 cfs (96 m^3/sec), and only eight have average discharges greater than 1,000 cfs (28 m^3/sec). The outlet is through the Straits of Mackinaw into Lake Huron; the mean discharge is 55,000 cfs (1,560 m^3/sec) (Powers and Ayers 1960). The lake's elevation above sea level averages about 579 feet (176.5 m).

Lake Michigan proper is divided into two rather distinct basins: the southern basin with a relatively smooth, gently sloping bottom and depths to 558 feet (170 m), and the northern basin with an irregular bottom and depth to 923 feet (281 m). The northern basin contains a number of islands. Almost the entire lake bottom is covered with glacial till or lake sediments (Hough 1958).

Much of the shore along the southern two-thirds of Lake Michigan is characterized by a smooth, unbroken shoreline, backed by gently rolling terrain; extensive dunes border the eastern and southern shores. The northern end of the lake has an irregular shoreline and in most places is bordered by hills. The southern part of the watershed is a mixture of farmland and urbanized areas, the central portion is primarily farmland, and the northern section is mostly forested. The largest city along the shoreline, Chicago, Illinois, is not considered to be in the watershed, because its drainage has been into the Mississippi River since the completion of the Chicago sanitary canal in 1900.

Green Bay, in northwestern Lake Michigan, is 118 miles (190 km) long and averages 23 miles (37 km) in width. It is generally more eutrophic and productive than the rest of the lake, and usually yields about half the lake's total annual catch of commercial fish.

Two small bays, Little Bay de Noc and Big Bay de Noc, are at the northern end of Green Bay. Grand Traverse Bay and Little Traverse Bay, the only other bays of consequence in Lake Michigan are in the northeast comer of the lake.

The average January temperatures at shore stations around Lake Michigan range from -4 to -9 C, and the average July temperatures from 20 to 23 C. Annual precipitation averages about 30 inches (76 cm); it is rather evenly distributed throughout the lake over the long term, but differs considerably in different areas of the lake in individual years. Winds are most often (at least 60%) from a westerly quadrant.

The following description of water temperatures in Lake Michigan is from J. F. Carr, J. W. Moffett, and J. E. Gannon (MS in preparation), and from unpublished data of the Great Lakes Fishery Laboratory.

The annual water temperature cycle consists of a 5-month warming period from middle or late March to middle or late August, and a 7-month cooling period. Thermal stratification does not develop until after mid-May, and is not stable until late June. Water temperatures are distinctly higher near shore than off shore through May but this difference is greatly reduced by late June, when the surface temperatures generally range from 15 to 20 C. The surface water is warmest in late July and early August, when temperatures of 20-25 C are common. At that time the epilimnion averages about 9-10 m in thickness, and the temperature gradient in the metalimnion is greater than 1 C/m. The epilimnion cools and thickens slowly in late August and early September, then rapidly from late September through November. By mid-November the surface temperature is about 10 C and the epilimnion is about 40 m thick. In mid-December the water temperature offshore decreases gradually from near 7 C at the surface to about 5 C at the bottom. In January-March the lake is vertically homothermous. Inshore temperatures are near 0.1 C. Offshore waters are warmer, but continue to cool throughout most of the period. In 1955, for example, temperatures at a station 15 miles (24 km) offshore were 4.2 C in January and 2.4 C in March. A large portion of Lake Michigan remains ice-free in winter, and large accumulations of ice are limited to shore zones, the extreme northern part of the lake proper, and Green Bay (which freezes over nearly every year).

Inshore temperatures are subject to frequent significant fluctuations in summer, particularly in August, due to the formation and dissipation of upwellings of various intensities. At a depth of 18 feet (5.5 m) off Saugatuck, Michigan, in August 1969, bottom water temperature changed as much as 10 C in 24 hours or less on three occasions, and as much as 3 C in 120 hours or less on 15 occasions.

Lake Michigan's waters are moderately hard. Total alkalinity (as $CaCo_3$) is 113 ppm; the concentrations of calcium, magnesium, and sodium are 31.5, 10.4, and 3.4 ppm, respectively; the phosphorus concentration is 0.9 ppb; and dissolved oxygen concentrations are near saturation at all depths (Beeton and Chandler 1963).

Lake Michigan's biota, except in southern Green Bay and areas around river mouths, is generally typical of that in North American oligotrophic lakes. Phytoplankton is dominated by diatoms; common oligotrophic diatom species are *Cyclotella comta, C. operculata,* and *C. ocellata* (Stoermer and Yang 1969). Invertebrate fauna is characterized by such oligotrophic forms as the amphipod *Pontoporeia affinis;* the mysid *Mysis relicta;* the copepods *Limnocalanus macrurus* and *Senecella calanoides;* and the oligochaetes *Stylodrilus heringianus, Peloscolex variegatus,* and *Limnodrilus profundicola. AU* of these invertebrates except *Senecella* are abundant. Many less highly oligotrophic benthic and planktonic forms also are common, however.

The original fish fauna of Lake Michigan included, among other species, 10 coregonines and 1 salmonine. The lake whitefish *(Coregonus clupeaformis),* the lake herring *(C. artedii),* and the lake trout *(Salvelinus namaycush)* were most abundant. Some of the coregonines have become rare or extinct, and several salmonines have been introduced. All common fish of Lake Michigan, past or present, are listed below. Excluded are a few species (characteristic of more eutrophic environments) that are occasionally common near river mouths or in certain areas of southern Green Bay.

Sea lamprey	*Petromyzon marinus*
Lake sturgeon	*Acipenser fulvescens*
Alewife	*Alosa pseudoharengus*
Lake whitefish	*Coregonus clupeaformis*
Blackfin cisco	*Coregonus nigripinnis*

. . . .	*Coregonus johannae*
Longjaw cisco	*Coregonus alpenae*
Shortjaw cisco	*Coregonus zenithicus*
Bloater	*Coregonus hoyi*
Kiyi	*Coregonus kiyi*
Shortnose cisco	*Coregonus reighardi*
Lake herring	*Coregonus artedii*
Round whitefish	*Prosopium cylindraceum*
Lake trout	*Salvelinus namaycush*
Brook trout	*Salvelinus fontinalis*
Rainbow trout (steelhead)	*Salmo gairdneri*
Brown trout	*Salmo trutta*
Coho salmon	*Oncorhynchus kisutch*
Chinook salmon	*Oncorhynchus tshawytscha*
Rainbow smelt	*Osmerus mordax*
Northern pike	*Esox lucius*
Carp	*Cyprinus carpio*
Emerald shiner	*Notropis atherinoides*
Spottail shiner	*Notropis hudsonius*
Longnose sucker	*Catostomus Catostomus*
White sucker	*Catostomus commersoni*
Channel catfish	*Ictalurus punctatus*
Bullheads	*Ictalurus* spp.
Trout-perch	*Percopsis omiscomaycus*
Burbot	*Lota lota*
Ninespine stickleback	*Pungitius pungitius*
Smallmouth bass	*Micropterus dolomieui*
Yellow perch	*Perca flavescens*
Walleye	*Stizostedion vitreum vitreum*
Freshwater drum	*Aplodinotus grunniens*
Slimy sculpin	*Cottus cognatus*
Spoonhead sculpin	*Cottus ricei*
Fourhorn sculpin	*Myoxocephalus quadricornis*

The common name of *Coregonus johannae* is sometimes listed as “deepwater cisco.” In this report, however, the ciscoes as a group (except for the lake herring sometimes called “shallow-water cisco”) are designated as “deepwater ciscoes”; to avoid confusion, we have not assigned a common name to *Coregonus johannae*. Of the species listed, northern pike, channel catfish, bullheads, and freshwater drum are restricted mostly to Green Bay, and smallmouth bass are confined mainly to certain shallow, rocky areas of northern Lake Michigan proper and northern Green Bay.

FACTORS THAT HAVE CAUSED CHANGES IN NATIVE FISH STOCKS AND OTHER BIOTA

General descriptions of the factors involved in changes in Lake Michigan are given here; their effects are discussed in later sections.

Exploitation

Exploitation of Lake Michigan's fish stocks has been almost altogether through commercial operations, but sport fisheries have at times been important, especially in recent years.

The commercial fishery

No attempt is made here to trace in detail the history of the commercial fishery; a summary of developments in the fishery (particularly in its earlier days), however, facilitates the later discussion of changes in the fish population. Most of these data, unless otherwise stated, are from Milner (1874), Smiley (1882), Smith and Snell (1891), and Baldwin and Saalfeld (1962 plus supplement 1970).

The date of first commercial fishing in Lake Michigan is not known, but it was at least as early as 1843. The fishery grew rapidly. In the beginning it was conducted mostly along shore with haul seines, but gill nets were introduced in 1846 or 1847 and pound nets about 10 years later. The use of gill nets and pound nets spread rapidly; they soon largely replaced haul seines and became, together with trap nets (introduced about 1885-Buettner 1965) the most important gears to the present time. Other gears, however, such as set lines, fyke nets, and trawls, have on occasion also been important.

The earliest fishery was primarily for whitefish, which were extremely abundant near shore. By 1860 certain grounds for this species already were becoming depleted and by the 1870's complaints about the scarcity of whitefish were common. Whitefish production, however, was still held at a high level-12 million pounds- in 1879 (the first year of record) by increased fishing effort, increased efficiency of gear (e.g., smaller meshes, finer twine in gill nets), and shifts to new fishing grounds. Total production for all species in that year (Fig. 2) was nearly twice the whitefish catch, because by that time lake trout, sturgeon, and lake herring had become important. Whitefish catches dropped abruptly soon thereafter but total production held rather stable until 1892 (average annual production 1879-92, 25.3 million pounds), due to increases in the catch of lake trout, lake herring, deepwater ciscoes, perch, suckers, and (to a smaller extent) walleyes. Total production jumped markedly to an average of 41.2 million pounds in 1893-1908, due mostly to increases in lake herring catches. The sturgeon ceased to be important during that period. Total production dropped abruptly between 1908 and 1911 (owing primarily to a decrease in the lake herring catches), but was rather stable at an average of 23.6 million pounds in 1911-42. During the latter period carp and smelt (both introduced) were added to the list of important species, and walleye production became rather low. Gallagher and Van Oosten (1943) listed the eight most important species, in order of yield and value, taken from Lake Michigan in 1939, as follows:

Order of yield	Order of value
Lake trout	Lake trout
Deepwater ciscoes	Deepwater ciscoes
Yellow perch	Yellow perch

Lake herring	Whitefish
Smelt	Lake herring
Suckers	Smelt
Carp	Suckers
Whitefish	Carp

Since 1942 the relative importance of the various species in the Lake Michigan commercial fishery has varied greatly. Important changes have been: a temporary drastic decrease in smelt production in the mid 1940's; the decline and elimination of the lake trout in the late 1940's and early 1950's; a great decrease in whitefish production in the middle and late 1950's, and some recovery in the 1960's; a substantially increased production of deep-water ciscoes beginning in the late 1940's; a brief, spectacular resurgence of walleye production from the late 1940's to the mid-1950's; and the appearance of the introduced alewife in the catches in the late 1950's and its extremely large production by the mid-1960's. In spite of these changes, total production did not vary markedly from the 1911-42 mean until 1966, when alewife catches became large. The average was 25.8 million pounds in 1943-65 and 50.5 million in 1966-70.

Throughout the history of the commercial fishery the efficiency of operation increased almost constantly. The changes in gill nets provide an example of these improvements. The earliest gill nets were constructed of coarse cotton webbing, with wooden-slat floats and stone weights. In the late 1800's cotton webbing gave way to finer linen twine, and wooden floats and stone sinkers to corks and leads. In the 1930's the linen webbing was replaced by more efficient flexible cotton, which in turn was replaced in the late 1940's and early 1950's by nylon. The earliest nylon nets were estimated to have been between two and three times as efficient in catching fish as the cotton nets they replaced (Hile and Buettner 1955). Improvements in nylon (e.g., monofilament construction) have been made in the past two decades. Over the history of the fishery, especially in the earlier years, there was a tendency toward smaller meshes and greater width in the gill nets. The range from home port was increased by a change from sailing vessels to power vessels (first steam tug in 1869) and the quantity of gill nets that could be set was increased by installation of power equipment for lifting the nets (beginning in the late 1800's).

At least as early as the 1870's many fishermen held the opinion that high production of certain species was being maintained only by increases in the efficiency and amount of gear fished. The same statement would apply to some extent throughout the history of the fishery, so that for some species the declines of abundance have been substantially greater than production figures indicate, including those figures based on catches per standard unit of fishing effort.

The sport fishery

Among the earliest references to sport fishing in Lake Michigan are statements by Smith and Snell (1891) that pleasure fishing was carried out by a great many people in the Chicago area in 1885. These anglers fished mostly from piers and wharves for yellow perch, using hand lines baited with

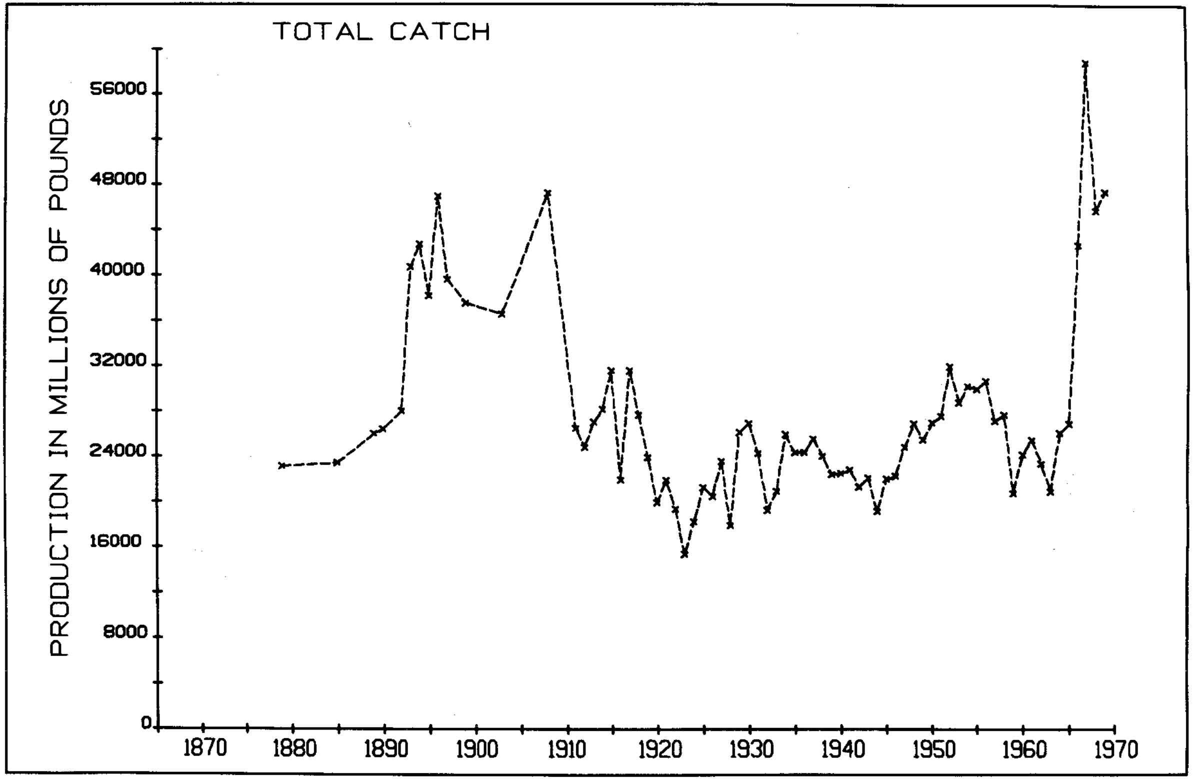

Figure 2. Total commercial production in Lake Michigan, 1879-1970.

minnows which also were taken from Lake Michigan. Although the history of the sport fishery is almost totally undocumented and few catch records have been kept until recently, it seems safe to assume that the yellow perch has been the most important species, considering the entire period. Until the past decade, most breakwalls around the lake were often lined with anglers fishing for yellow perch. The walleye also has been a favorite of sport fishermen. This species has been caught mostly in Green Bay, where it was taken in huge numbers in the 1950's. Smelt are caught throughout Lake Michigan (almost entirely in shallow areas or in streams during the spawning run), but mostly in the northern portion. The sport fishery for smelt was perhaps at its peak in 1942, when more than 5 million pounds were taken from Michigan waters of the lake alone-as compared with perhaps 200,000 pounds or less in 1970 (2.8 million fish; weight unknown). Trolling for lake trout was popular in Grand Traverse Bay before the collapse of this species in the late 1940's.

In recent years the intensive stocking of salmonids has led to the most spectacular sport fishery in Lake Michigan's history. The angling is for coho and chinook salmon and lake, steelhead, brown, and brook trout. An example of the magnitude of the sport fishery is given by these catches in 1970 in State of Michigan waters alone: 500,000 coho salmon, 275,000 steelhead trout, 229,000 lake trout, and 170,000 chinook salmon (unpublished records, Michigan Department of Natural Resources). Some brown trout and brook trout also were taken, but more of these are caught in Wisconsin waters, where they were stocked more heavily.

Smallmouth bass provide a lively sport fishery in certain shallow rocky areas of northern Lake Michigan. Also taken in limited numbers, mostly in Green Bay, are northern pike, rock bass *(Ambloplites rupestris)*, and a few other warmwater species.

Introduced fish species

Exotic fish species have become extremely important in Lake Michigan. Their early histories and later fluctuations in abundance are described briefly here:

Carp

The time of the carp's first appearance in Lake Michigan is not known. Commercial production records started in 1893, with an entry of only 2,000 pounds, and by 1899 the catch had increased only to 25,000 pounds (Fig. 3). Production was nearly 0.5 million pounds in 1908 and passed 1 million pounds in 1934. The annual average was 1.5 million pounds in 1934-65 and 2.3 million in 1966-70. Although it may be assumed that the small catches before 1900 reflect the low abundance of carp soon after its introduction and that the great increase in catch soon after 1900 resulted from rapid increases in carp population, later changes in production have followed changes in market demand rather than abundance. A large proportion of the catch has been from southern Green Bay, although some carp are taken in nearly all shallow areas of the lake, particularly in the southeastern portion. Although the effects of carp (e.g., uprooted vegetation and muddied water) often

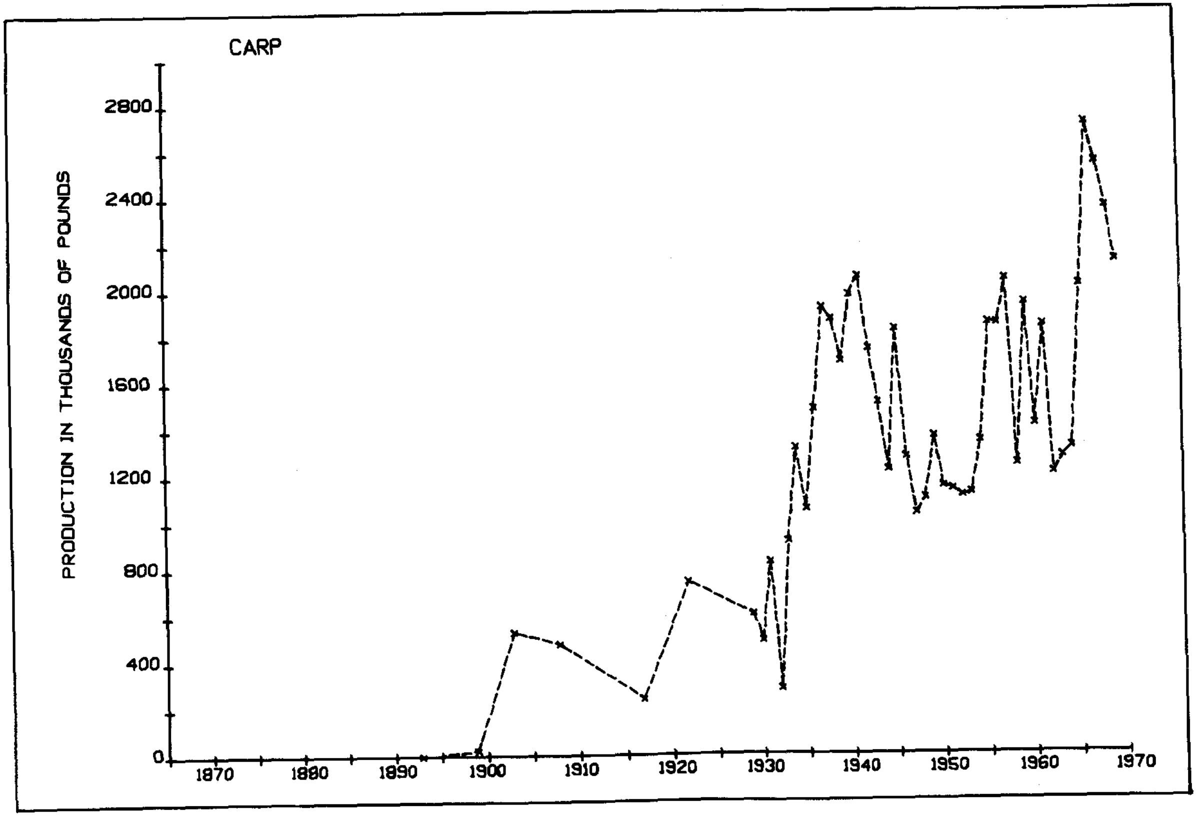

Figure 3. Commercial production of carp in Lake Michigan, 1893-1970.

reported in other bodies of water are not documented for Lake Michigan, it seems likely that the carp did cause certain changes injurious to native fauna in some areas of Lake Michigan, particularly Green Bay.

Smelt

The smelt in Lake Michigan originated from a planting in Crystal Lake, Michigan, in 1912 (Van Oosten 1937). The first smelt reported in Lake Michigan was caught in a commercial net in 1923 off Frankfort, Michigan, which is at the mouth of the stream through which Crystal Lake drains into Lake Michigan. By 1924 smelt had crossed Lake Michigan into Green Bay, and by 1936 they occupied the entire lake.

Commercial production of smelt increased from 86,000 pounds in 1931 (the first year of record) to 4.8 million pounds in 1941 (Fig. 4). The take then dropped abruptly to 2.2 million pounds in 1943 and 5,000 pounds in 1944 but recovered quickly to 1.1 million pounds in 1948 and reached a record 9.1 million pounds in 1958. Catches again dropped thereafter to 927,000 pounds in 1965 but increased steadily to 2.5 million pounds in 1969. Since 1953 (when the records first indicated the proportion of the catch from Green Bay), 72-98% of the annual commercial production has been in Green Bay.

The abrupt decline of smelt production in Lake Michigan in 1943 and 1944 was the result of a mass mortality (apparently caused by disease) in the winter of 1942-43 (Van Oosten 1947). The fairly substantial catch of 1943 was made in winter, before the dieoff had ended; by spring, few smelt remained in Lake Michigan. That the smelt population was enormous just before the dieoff is indicated by the dip net catch by sport fishermen in 1942, which was estimated at 5.5 million pounds in State of Michigan waters and was probably nearly that high in Wisconsin (Van Oosten 1947). It seems probable, therefore, that numbers of smelt were greater in the first peak production year of 1941 than in the record year of 1958, even though the 1941 commercial production was only about that of 1958.

Although the decline of smelt in 1959-65 probably was not as great as production figures indicate (reduced market demand influenced the catch), a substantial decline unquestionably occurred. Smith (1970) attributed the decrease to the alewife, although he believed (on the basis of information from other lakes) that alewives have less effect on smelt than on certain other species. Consequently, other important factors may also have been involved in the decline.

Effects of smelt on native stocks are not obvious, but it is difficult to imagine that an exotic which reached the abundance of smelt in Lake Michigan would not have exerted at least some influence. Evidence exists that smelt adversely affected lake herring (discussed later), and there is no question that smelt have provided valuable forage for lake trout (Wright 1968).

Sea lamprey

The sea lamprey almost certainly has had a greater influence than any other exotic on the native fish stocks of Lake Michigan. Its most conspicuous

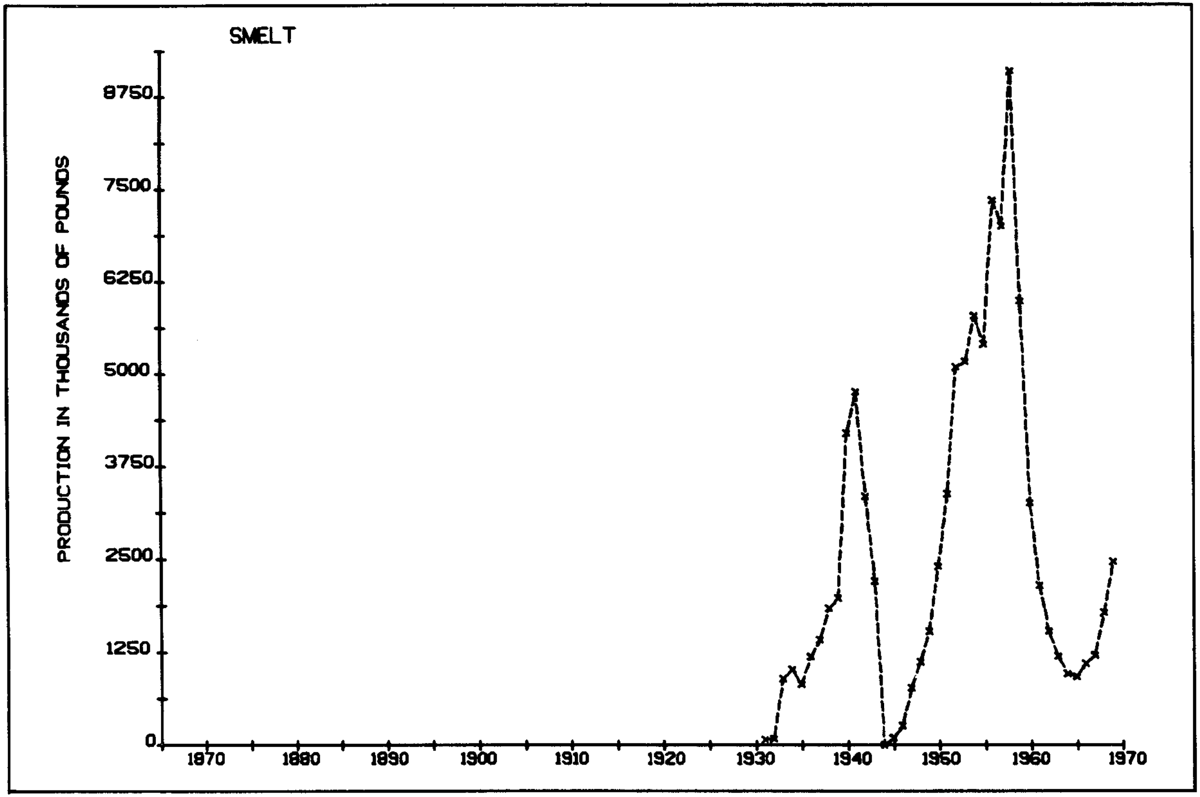

Figure 4. Commercial production of smelt in Lake Michigan, 1931-70.

effects have been in direct attacks on native species, but Smith (1970) believed that the destruction of predators by the lamprey allowed the invasion of another exotic, the alewife, which influenced native stocks still further. The first reports of this parasite in Lake Michigan were in 1936, when specimens were taken at several widely scattered localities (Applegate 1950). A decade later the sea lamprey was firmly established-spawning runs had been reported in many streams and commercial fishermen had for several years complained of high incidences of sea lamprey wounds on the fish in their catches (Shetter 1949).

Early reports indicated that the sea lamprey's primary victim was the lake trout, followed by whitefish, suckers, walleyes, yellow perch, and carp (Shetter 1949). Other species, particularly deepwater ciscoes and burbot, have also been severely attacked. Smith (1968) estimated that during its maximum abundance in Lake Michigan in the mid-1950's the sea lamprey destroyed 5 million pounds of fish per year, mostly deepwater ciscoes (by this time few lake trout remained).

Sea lamprey control efforts began in Lake Michigan in 1953 (several experimental control devices had been installed in 1952). By 1958, barriers (mostly electrical, a few mechanical) had been placed across 65 streams to block upstream migrations of sea lampreys. Barrier operations were discontinued in 1960 in favor of a much more effective method of lamprey control-the treatment of streams with a toxicant selective for lamprey larvae. All tributary streams known to harbor sea lamprey larvae had been treated by 1966, and many of the streams have since been treated a second time. The success of the treatment is shown by the sharp decline of spawning-run sea lampreys at three barriers which had been left in operation to provide yearly indices of abundance: 12,886 lampreys were caught in 1961 and 1,168 in 1966. Due to budgetary limitations the "index" barriers were removed after the 1966 spawning season; consequently, trends in lamprey abundance since that time are not easily ascertained. Reduced wounding rates for lake trout between 1969 and 1970, however, are encouraging.

Alewife

The first alewife recorded in Lake Michigan was taken in the northeastern portion in 1949 (near the source of introduction from Lake Huron); by 1953 the species was dispersed throughout most of the lake (Miller 1957). The population increased rapidly, first in the northern segment. Fairly large numbers of adults and several schools of young were seen in Green Bay in 1953 (Joeris and Karvelis MS 1962). By 1956 fishermen in Green Bay were taking large quantities in pound nets fished for other species. In September 1955 one of us (Wells) observed large numbers of young alewives in the Manistique River, a tributary along the north central shore of the lake. Although at that time alewives were fairly common throughout northern Lake Michigan (unpublished data, Great Lakes Fishery Laboratory), the greatest concentrations were almost certainly in Green Bay.

Alewives were scarce in southern Lake Michigan until about 1956; only two adults are known to have been caught in 1953 and several in 1954 (Miller 1957). The first young were received by the Chicago Natural History Museum in October 1956 (Woods 1960), and by the winter of 1956-57 commercial fishermen in southern Lake Michigan were complaining about large numbers of alewives fouling their gill nets set for chubs (Miller 1957).

In the late 1950's and early 1960's the population increase of alewives in Lake Michigan was explosive. Commercial production increased from 220,000 pounds in 1957 to 4.7 million pounds in 1962 and reached a peak of 41.9 million pounds in 1967 (Fig. 5). Commercial production of alewives is so strongly influenced by market demands that catch figures are not necessarily accurate indicators of abundance, but experimental catches by the U.S. Fish and Wildlife Service R/V ***Cisco*** in southern Lake Michigan show similar striking increases in 1962-66 (comparable data not available before 1962).

The nuisance aspects of the alewife in Lake Michigan have attracted wide public attention. When alewives are concentrated along shore in spring they often cause extreme difficulties by clogging intakes of steel mills, power plants, and municipal water filtration plants, and by dying in huge numbers and collecting in windrows on beaches. The first spring dieoff of alewives in Lake Michigan for which an account was published was in the Chicago area in 1957 (Woods 1960). The number of dead fish was small (Loren Woods, personal communication), and it seems likely that small unreported spring mortalities may have occurred in northern Lake Michigan before 1957. Spring mortality became increasingly severe in Lake Michigan in the early 1960's, and an enormous dieoff occurred in 1967 (Brown 1968). On the basis of aerial observation and counts along small segments of beaches in various areas, U.S. Fish and Wildlife Service biologists estimated that mortality at several billion fish.

Catches per unit of effort in commercial and experimental trawls (the latter by the Great Lakes Fishery Laboratory) in the falls of 1966 and 1967 suggested that about 70% of the alewives in Lake Michigan died during the 1967 dieoff. (E. H. Brown, MS in preparation). Production was high in 1967 because much fishing effort had been expended before the dieoff. Both experimental and commercial catches indicated a further decline in numbers in 1968 (commercial catches dropped to 27.2 million pounds), and modest increases in 1969 and 1970 (production 33.5 million pounds in 1970).

The alewife unquestionably has had detrimental effects on native fish stocks, probably mostly by competition with the young for planktonic food or by predation on the young. Wells (1970) showed that alewives have had a strong influence on zooplankton in Lake Michigan (discussed in a later section). On the other hand, the alewife, as a prolific forage fish, has made possible the outstandingly successful salmon stocking programs in Lake Michigan in recent years.

Salmonines

Although introductions of salmonines into Lake Michigan began about a century ago, their greatest importance by far has been in recent years. Earliest releases (nearly all fry) included several species of salmon and trout, and were for the purpose of establishing naturally spawning populations. Except for rainbow trout and perhaps brown trout, however, the attempts were unsuccessful. Plants in the past decade (all fingerlings or yearlings) have been

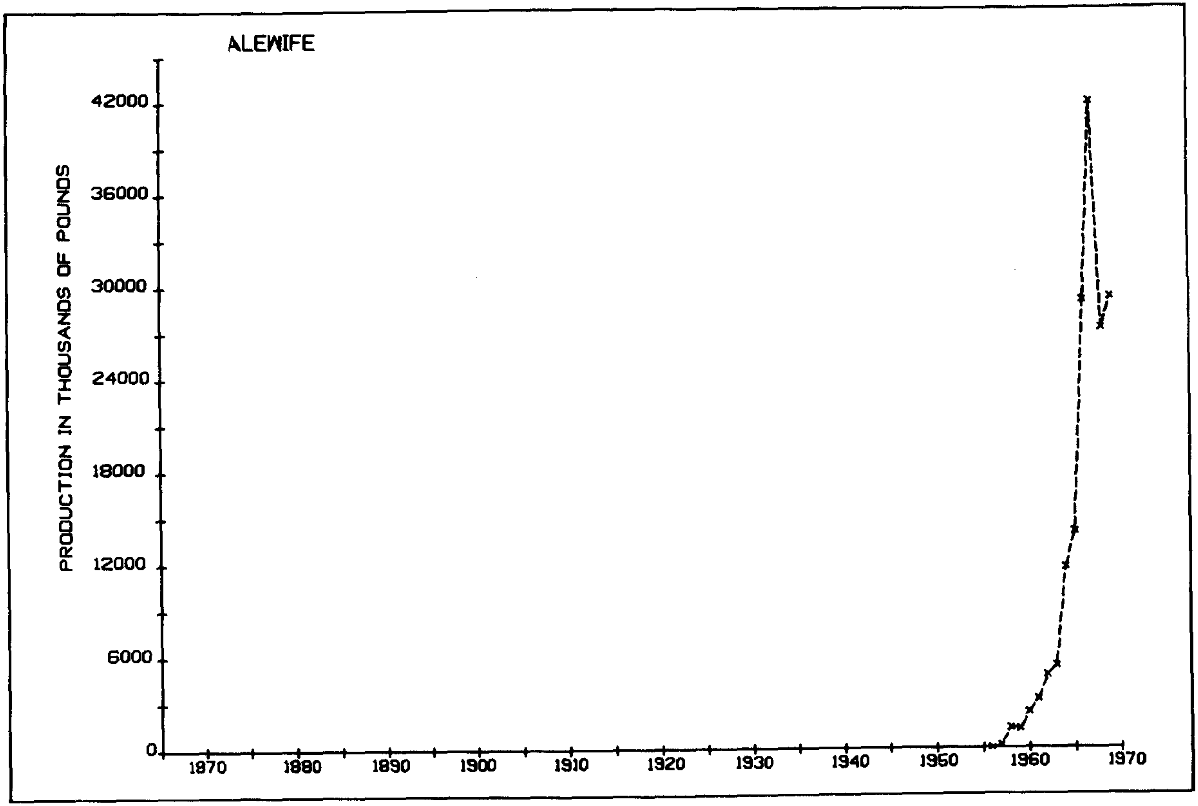

Figure 5. Commercial production of alewife in Lake Michigan, 1956-70.

designed mostly for a put-and-take sport fishery. The following statistics on salmonines have been taken from various reports of the U.S. Fishery Commission, the Michigan Department of Conservation (now the Department of Natural Resources), and the Great Lakes Fishery Commission, and from unpublished data of conservation agencies of the various states bordering Lake Michigan.

Early Pacific salmon introductions included 813 chinook salmon between 1873 and 1880, and 2,000 masu salmon (Oncorhynchus *masou)* in 1920. A large-scale program for the introduction of Pacific salmon into Lake Michigan began in 1966, when 660,000 coho salmon yearlings were released; a total of 10.3 million had been stocked through 1970. Extensive chinook salmon stocking began in 1967, and by the end of 1970, 4.1 million fingerlings had been released. The State of Michigan, which initiated the Pacific salmon program, released 94% of the coho salmon and 93% of the chinook salmon planted through 1970, but all the other states bordering Lake Michigan have participated in the stocking effort.

The success of the recent salmon program in Lake Michigan has been spectacular. In 1970 anglers in State of Michigan waters caught an estimated 500,000 coho and 170,000 chinook salmon, Of the coho salmon stocked in 1966, 1967, and 1968, the percentages ultimately either caught by fishermen or recovered at weirs on spawning streams were 32, 19, and 25, respectively. Equivalent figures cannot be given for chinook salmon because some of those from even the first planting presumably still had not spawned in 1970; 20% of the 1967 plant had been recovered by 1970, however. Growth of salmon has been excellent. Adult coho salmon weighed an average of 9.5 pounds in spawning runs of 1967, 1968, and 1969. In 1970 a world record coho salmon (33 pounds, 8 ounces) was taken. Twenty-pound chinook salmon were not uncommon in 1970, and a few caught by anglers weighed more than 30 pounds.

The first rainbow trout introduction of record into Lake Michigan tributaries was in 1880, but it is not clear whether these fish were from sea run “steelhead” stock or from nonmigratory strains. The first planting of fish specifically designated as “steelheads” was in 1896, when 10,000 yearlings were released in State of Michigan waters. Steelheads were stocked in most years thereafter until about 1915. From 1915 to 1960 few steelheads were planted, but since that time introductions have increased greatly. All states bordering Lake Michigan are now stocking rainbow trout. The program has been highly successful; an estimated 275,000 (many no doubt naturally spawned) were caught in State of Michigan waters alone in 1970.

A plant of 5,000 brown trout was made as early as 1883, and several hundred thousand brown and brook trout (mostly brown trout) have been stocked in Lake Michigan since the mid-1960’s. Both species have provided a successful sports fishery, particularly in Wisconsin waters where most of the plants have been made.

Stocking of Atlantic salmon *(Salmo* salar) in Lake Michigan began in 1872 and continued intermittently until 1932, by which time a total of 645,000 had been released. The program was largely unsuccessful. None have been stocked in recent years.

The direct influence of the introduced salmonids on native fish stocks has probably been only negligible. It seems safe to assume, however, that in recent years they may have affected the abundance of alewives, their main item of diet, and in doing so may have affected some native species that have important interrelations with the alewife. Although alewives increased in 1969 and 1970, it seems at least possible that they would have increased considerably more in the absence of the heavy predation by the introduced salmonids.

Accelerated eutrophication and other forms of pollution

A noticeable deterioration of Lake Michigan's environment (in certain inshore areas) began at least as early as the mid-1800's, when sawdust and other refuse discharged from sawmills into tributary streams often floated out into the lake and sank (Milner 1874). By 1885 the Milwaukee River had become so polluted (probably by several contaminants) that few fish entered it (Smith and Snell 1891). Deforestation, drainage, and construction of dams, although not strictly "pollution," also must have affected Lake Michigan's fish stocks by blocking migration or by causing warming of the water in the streams and their estuaries. An expanding human population has discharged increasing amounts of domestic and industrial wastes and other pollutants into the lake. The most heavily polluted area is southern Green Bay, a large area of the bottom of which is covered with anoxic gray sludge (Edgington and Callender 1970).

Changes in certain chemical components of Lake Michigan are substantial enough to indicate that eutrophication has been accelerated to at least some extent by man. Beeton (1969), who analyzed all available records through 1966, showed that total dissolved solids increased by 30 ppm, sulfates by 13 ppm, and chloride by about 6 ppm during the preceding 90 years, and organic nitrogen increased and inorganic nitrogen decreased during the preceding 38 years; data were lacking for an analysis of changes in phosphorus. Oxygen levels have decreased greatly in southern Green Bay, and possibly also to some extent in the rest of the lake. Minimum oxygen concentrations in southern Green Bay declined from 2-3 ppm in 1938-39 to only 0.0-1.0 ppm in 1955-56 (Beeton 1969). Oxygen concentrations in the main body of Lake Michigan remain near saturation, although Ayers, Stoermer, and McWilliam (1967) believed that oxygen concentrations decreased somewhat in a part of northern Lake Michigan between 1955 and 1966. Records of the Great Lakes Fishery Laboratory do not indicate any change in the southern portion of the lake between 1954 and 1968. Schelske and Stoermer (1970) reported that silica has decreased in the southern part of Lake Michigan at an average rate of 0.1 ppm per year in the past 40 years. They attributed this decrease to an increase in the abundance of certain diatoms that are favored by eutrophication.

Toxic trace elements in Lake Michigan have received attention in several recent studies. Mercury concentrations in Lake Michigan fish have been generally low but values up to 0.82 ppm have been reported for deepwater sculpins in the open lake (Edgington, Thommes, Gassman, and Cutler 1970) and up to 0.75 ppm for unspecified species in Green Bay (Kleinert and Degurse 1971). Edgington and Callender (1970) reported mercury concentrations to be great enough (2.95 ppm) in anoxic sludge of southern Green Bay to suggest a high degree of mercury pollution in that area (levels are much lower in northern Green Bay). Methodology for mercury analysis, however, apparently has not progressed to the point that published figures can be considered absolutely reliable. Selenium, which falls into the lake in ash residues from burned fossil fuels, has been observed in rather high concentrations in zooplankton, especially in the southern part of the lake (Copeland 1970).

Lake Michigan has been subjected to considerable insecticide contamination. On the basis of concentrations in fish, insecticide levels in Lake Michigan are the highest in any of the Laurentian Great Lakes (Reinert 1970). Contamination, which is mostly by DDT and to a lesser extent dieldrin, is heaviest in the southern part of the lake. Insecticide levels fortunately do not appear to have increased further in Lake Michigan between 1967 and 1970 (unpublished data, Great Lakes Fishery Laboratory).

Thermal pollution in Lake Michigan, as in many other bodies of water, has become a subject of increasing public concern. Most of the heated effluents are from one nuclear and 23 fossil fuel power plants; seven additional plants (five nuclear and two fossil fuel) are scheduled for operation by 1974. Steel mills also contribute to the thermal input of Lake Michigan. The artificial heat input is now only a small portion of the total for Lake Michigan, but in the year 2000 it will be an estimated 11 times the level of 1968 (Acres 1970). Detrimental effects which are probably localized at present may therefore be expected to spread. Environmentalists are clamoring for legislation requiring closed cooling systems for all power plants put into service in the future (and for some of the largest now operating) on Lake Michigan.

CHANGES IN BENTHOS AND PLANKTON

Although limnological studies in Lake Michigan have proliferated in the past decade, a detailed assessment of changes in benthos and plankton is difficult due to a scarcity of earlier data with which to make comparisons. Enough data are available, however, to permit a limited evaluation of some of the more prominent changes.

Benthos

Some changes in Lake Michigan benthos in the past several decades have been documented; all have been attributed to accelerated eutrophication or other pollution.

Conspicuous changes in benthos have occurred in southern and central Green Bay (Beeton 1969 and Howmiller and Beeton 1970). Nymphs of the burrowing mayfly, *Hexagenia,* were common in 1939 but were rare in 1952 and absent by 1955. Oligochaetes and chironomids increased between 1939 and 1969, except for a decrease near the mouth of the Fox River (a large, grossly polluted tributary). Amphipods, leeches, snails, and fingernail clams were less abundant in 1969 than in 1952.

Changes in bottom fauna probably also have occurred in many shallow areas of the main body of Lake Michigan. Cook and Powers (1964) have shown differences between the benthos off the mouth of the St. Joseph River (which flows into Lake Michigan at St. Joseph) and an inshore area not near a major tributary, and attributed these differences to the greater inflow of suspended solids from the river. The benthos at the mouths of all major tributaries to Lake Michigan probably has changed, since the suspended solids of these rivers almost certainly have increased.

Robertson and Alley (1966) reported significantly larger numbers of oligochaetes and the amphipod *Pontoporeia affinis* in the southern two-thirds of Lake Michigan in 1964 than in 1931. Fingernail clams (Sphaeriidae) probably also were more abundant in 1964. The authors interpreted the increase in all three dominant benthos groups as a suggestion of a long-term trend, but believed that definitive conclusions were not possible on the basis of only 2 years' data because the abundance of benthic organisms may vary greatly from year to year, even in the absence of such trends.

In spite of the evidence of trends toward eutrophication, the presence of the oligochaete *Stylodrilus heringianus* and *Peloscoiex variegatus* (Hiltunen 1967) the midge *Heterotrissocladius subpilosus* (Henson 1966) and the fingernail clams *Pisidium coventus* and *Sphaerium nitidum* (Herrington 1962) indicate that the benthos of the open areas of Lake Michigan retain a strongly oligotrophic character.

Zooplankton

Zooplankton populations in Lake Michigan have changed strikingly in recent years, as indicated by collections made in 1954, 1966, and 1968 (Wells 1970). Sharp declines in abundance occurred between 1954 and 1966 in the three largest cladocerans, *Leptodora kindtii, Daphnia galeata,* and *D. retrocurva,* and the four largest common copepods, *Limnocalanus macrurus, Epischura lacustris, Diaptomus sicilis,* and *Mesocyclops edax. Daphnia galeata* and *Mesocyclops edax* were almost eliminated. At the same time most of the remaining zooplankton species increased in abundance. Between 1966 and 1968 the composition of zooplankton populations shifted generally back toward that of 1954. Wells attributed the changes to differences in the abundance of alewives as described earlier; this planktivore, which has been shown to select the larger species of zooplankton (Brooks 1968) increased phenomenally in abundance between 1954 and 1966, then declined drastically by 1968.

A conspicuous zooplankton change in Lake Michigan probably not related to the above events has been the recent invasion of the brackish water copepod, *Eurytemora affinis* (Robertson 1966).

An accurate comparison of present zooplankton populations in Lake Michigan with those before 1954 is not possible. Although one major earlier study, based on samples collected in 1887-88 and 1926-27, was published (Eddy 1927), collection methods were much different from those used in later work. Eddy's samples were from the surface near shore (mostly from a Chicago breakwall), whereas later collections were from various strata offshore. Nevertheless, considerable attention has been given to the difference in abundance of *Bosmina coregoni* as reported for 1886-87 and 1926-27 (the most abundant cladoceran) and for 1954 (absent-Wells 1960). Beeton (1965) interpreted these differences as an indication of eutrophication; Brooks (1969) related them to a decrease in planktivorous fish, which permitted large zooplankton species to proliferate and completely exclude the smaller *B. coregoni.* The reappearance of *B. coregoni* in 1966 after intense alewife predation had decimated large zooplankters (Wells 1970), would seem to refute Beeton's argument and lend support to that of Brooks. Wells (1970) however, questioned whether there is a real basis for comparison, in light of the confusion in taxonomy of the genus.

Gannon (1970) showed marked differences in the species composition and abundance of crustacean zooplankton between southern Green Bay and the rest of Lake Michigan (including northern Green Bay), and suggested that the differences might be due in part to accelerated eutrophication, and consequent zooplankton changes, in southern Green Bay; proof is lacking, however, because no comparative data for earlier periods exist for southern Green Bay. Gannon's study also indicated that the effect of alewife predation on zooplankton populations has not been as pronounced in southern Green Bay (where, for example, *Mesocyclops edax* is still common) as elsewhere in the lake.

Phytoplankton

The phytoplankton of Lake Michigan has undergone some distinct changes since the 1800's, which have been attributed to accelerated eutrophication and other forms of pollution.

Stoermer and Yang (1969) studied changes in Lake Michigan diatoms (which have dominated the phytoplankton) by comparing data from several reports, dating back to 1872, with their own findings in extensive collections of 1964 and 1967; the following summary is from their review. The diatom flora of Lake Michigan is becoming more diverse. Certain taxonomic entities *(e.g., Stephanodiscus binderanus)* associated with moderate to high levels of pollution apparently were not present until about the 1930's; they are now abundant in certain inshore areas and are becoming increasingly common offshore. Members of the genera *Thalassiosira* and *Coscinodiscus,* indicators of extreme water quality degradation in the Great Lakes, came into Lake Michigan between 1947 and 1964; at the present time their distribution is highly restricted. On the basis of plankton diatom assemblages, the areas of greatest environmental disturbance in Lake Michigan are: the southern portion of Green Bay; the extreme southern crescent of the lake from Chicago, Illinois, to Benton Harbor, Michigan; the northeastern coast from Ludington to Frankfort, Michigan; and local areas near most major harbors. In the offshore areas certain strongly oligotrophic diatom species, such as *Cyclotella comta, C. operculata,* and *C. ocellata,* are still present, although their numbers are reduced-especially in the southern portion of the lake.

Although A. M. Beeton (MS in preparation) did not directly compare past and present data, he believed that the substantial differences in diatom species, abundance, and generation times (i.e., average doubling times for the populations) between offshore and inshore areas (particularly southern Green

Bay) of Lake Michigan (reported by Holland 1969), reflect changes in the inshore areas. Beeton implies that increased enrichment due to man's activities (which has the greatest effect in inshore areas) has made the inshore-offshore differences greater than in the past.

Schelske and Stoermer (1970) believed that, although a decrease in silicon in the past 40 years (mentioned in an earlier section) resulted from an increase in certain diatoms favored by eutrophication, some of the diatoms are not being replaced in the Lake Michigan phytoplankton assemblage by blue-green and green algae. The literature provides only limited further data for comparisons of present nondiatom phytoplankton with that of the past in Lake Michigan. Beeton (1969) reported the presence of the blue-green alga *Aphanizomenon* in 1938-1939 (blooms) and *Schizothrix* in 1952 and 1963-65 in Green Bay, and implied that these species were absent or less abundant formerly. The obnoxious green alga *Cladophora* unquestionably has increased, but it is found only in local areas of heavy pollution rather than widely as in Lakes Erie and Ontario (Beeton 1966).

CHANGES IN NATIVE FISH STOCKS

Lake Michigan's native fish stocks have changed vastly, and almost constantly in the last 120 years, far beyond what might be expected in normally fluctuating populations. Man's activities have been responsible, either directly by exploitation, or indirectly by eutrophication (and other pollution) or by causing conditions which led to the invasion of exotic fish species. Until the early 1920's when the smelt first entered Lake Michigan, only exploitation and pollution (and probably drainage, deforestation, and damming, which led to warming or blocking of spawning streams) were affecting fish stocks significantly. The species introduced before the smelt-salmonines (mostly unsuccessful) and carp-probably exerted little influence. Since the smelt's introduction, all three factors-exploitation, pollution, and exotic species-have been involved.

It is impossible, of course, to separate precisely the influence of the various factors on changes in Lake Michigan's native fish stocks. Opinions on the relative importance of the various factors, in fact, have varied over the years during which changes have been noted. Until about the mid-1940's, the prevalent opinion was that overexploitation was responsible for most of the changes, the most obvious of which were decreases in abundance of desired species. Most of the earliest commercial fishermen, observing marked declines in their favored species (particularly whitefish) were among the first to express this view, although they also recognized the adverse effects of pollution. Scientists investigating the early declines in commercial species agreed with these fishermen (see Milner 1874; Smith and Snell 1891). Some fishery scientists in the 1920's, 1930's, and early 1940's were vehement in their belief that declines in stocks of desired species in Lake Michigan and other Great Lakes were almost altogether a result of commercial overexploitation (see, e.g., Van Oosten 1938, 1939). Since that time a common, though by no means universal, opinion among fishery scientists has been that exploitation was overemphasized as a factor in the earlier declines, and that the fishery has had almost no effect on recent changes.

Following is a species-by-species discussion of changes in the abundance of common native fish of Lake Michigan. For the most part we have regarded total production figures (mostly from Baldwin and Saalfeld 1962, plus supplement 1970) as indices of abundance. The weaknesses in this procedure are obvious (e.g., changes in fishing intensity are not taken into account) but we believe that production has usually provided a reasonably accurate index of major changes in abundance.

Whitefish

The whitefish was the mainstay of the early fishery in Lake Michigan (data on the early fishery are from Milner 1874 and Smith and Snell 1891). It was easily taken in large quantities even in shore seines, and was considered to have the finest flavor-superior to lake trout-in the salted product which was commonly used at that time.

Early accounts clearly indicate a substantial decline in the abundance of whitefish well before commercial production figures were available; increased fishing intensity and more efficient nets were required to maintain the catch. The decrease began in some areas along the west shore as early as the 1850's. Milner estimated a drop in abundance along the west shore and in Green Bay of "all of 50 percent" in the 10 or 12 years just before 1872. Milner's estimate was for whitefish and lake trout combined, but a consideration of the priorities of the fishery at that time leaves little doubt that his assessment was influenced mostly by whitefish. By 188.5 abundance had been severely reduced in many areas, particularly in Green Bay.

The earliest figures related to the commercial production of whitefish in Lake Michigan are for 1879 and 1885, when the combined catches of whitefish, round whitefish, and the large deepwater ciscoes (Coregonus ***nigripinnis*** and ***C. johannae)*** were 12.0 and 8.7 million pounds, respectively (Fig. 6). Whitefish undoubtedly made up the bulk of these catches. Van Oosten, Hile, and Jobes (1946) reported that whitefish constituted about three-fourths of the total catch of the above species in 1890; statements by Smith and Snell (1891) regarding changes in the fishery suggest that the proportion of whitefish was at least as great in 1879 and 1885. Production figures for whitefish alone begin with 1889, when the take was 5.5 million pounds. In 1892 production had dropped to 2.8 million pounds, and the average for 1892-1908 was 2.4 million. In 32 of the 43 years from 1911 to 1953, production was between 1.0 and 2.6 million pounds. Periods of significantly higher production were in 1928-32 (peak, 5.4 million pounds in 1930) and 1947-49 (peak, 5.8 million pounds in 1947). Production continued to drop more or less steadily after 1949 (abruptly after 1952) to an average of only 40,000 pounds in 1956-59, and then began a somewhat erratic but substantial increase to 1.7 million pounds in 1970.

The conspicuous decline of whitefish abundance in the years before 1885 was attributed by early investigators and fishermen to overfishing and pollution from sawmills (Milner 1874; Smith and Snell 1891). Overfishing seems to have been judged the more important. Justification for this view was based on the rapid decrease of whitefish in successive areas of increased fishing intensity, on the appreciable decline in the average size of the fish in

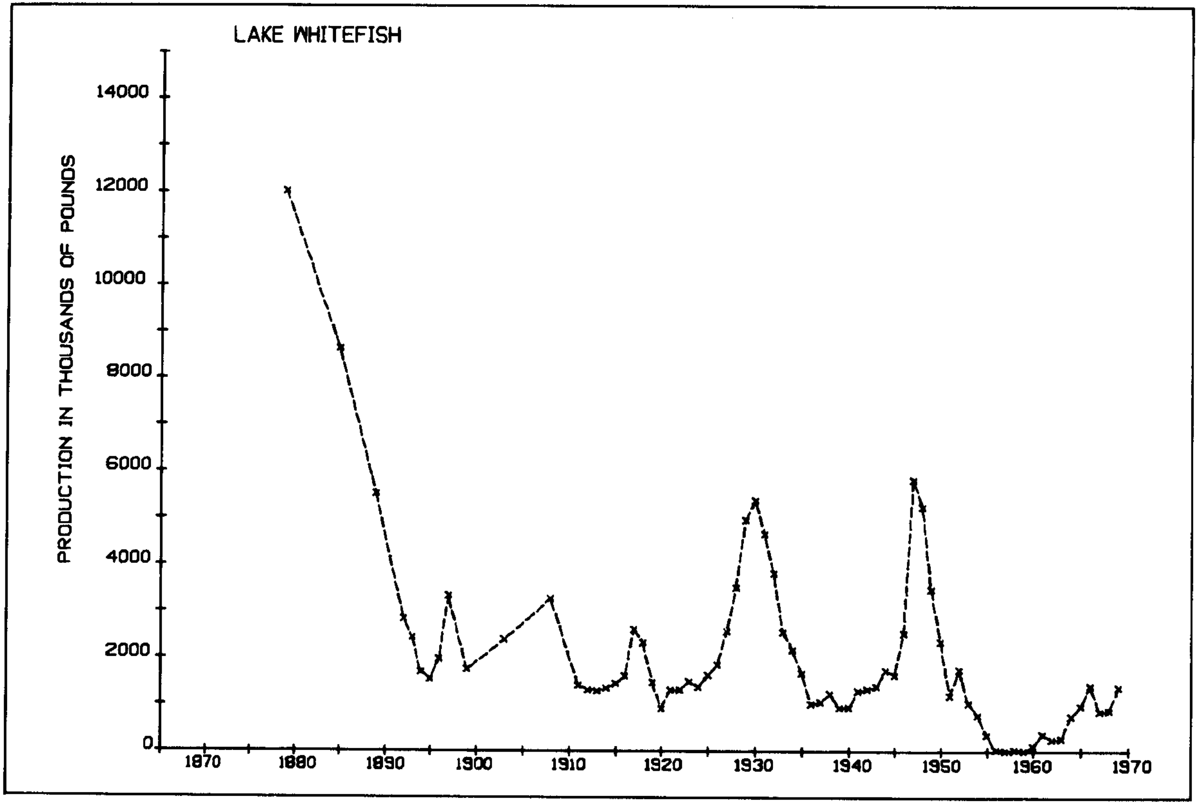

Figure 6. Commercial production of whitefish in Lake Michigan, 1879-1970.

the catch, and (by inference) on the wholesale slaughter of small whitefish. Koelz (1929), referring to the early exploitation of whitefish wrote, “At no season was the pursuit relented, and no fish were too small to be taken. The smallest, together with the herring and the sturgeon, often were carried out onto the beach (i.e., destroyed rather then released alive) because they were so numerous that they interfered with the capture of the larger whitefish. Though originally whitefish were found in incredible abundance all along the shore of the lake.. . they could not endure long such drains on their numbers.” Regarding sawmill pollution Milner wrote “The refuse from the sawmills . . . is thrown into the streams in immense quantities to float out and sink in the lake. It is having a very injurious effect on the fisheries. The water-logged slabs . . . tear and carry away the nets. The sawdust covers the feeding and spawning grounds of the fish.. . .” Complaints about sawdust were common on both sides of the lake; many of the whitefish spawning areas in streams (some, particularly in Green Bay, were entered for spawning in the early days) and in the lake near river mouths must have been destroyed. Although not mentioned specifically by early investigators, other forms of stream degradation must also have been locally detrimental to whitefish.

The increased production of 1928-32 probably resulted from a single exceptionally strong year class and the high yields of 1947-49 are known to have been sustained mostly by a single year class-that of 1943 (Mraz 1964). It is not likely that the gain in abundance in either period was directly proportional to the increase in production, for-as Van Oosten, Hile, and Jobes (1946) pointed out-better fishing is apt to invite heavier fishing intensity. The reason for the unusual success of the year class (or classes) that supported the high 1928-32 yield is not apparent, but we are tempted to suggest that a contributing factor to the success of the 1943 year class was the phenomenal decline of smelt in the winter of 1942-43 (which would have left whitefish fry free of possible interference from smelt in 1943). Both periods of high abundance were short. Increased exploitation (including limited use of the allegedly destructive deep trap net) was implicated to some degree in the rapid decline in 1928-32 (Van Oosten, Hile, and Jobes 1946); and we suspect that the marked rise in fishing intensity in 1947-49 (Hile, Lunger, and Buettner 1953) also exacted its toll, and led to a considerably faster decline than would otherwise have occurred. Cucin and Regier (1966) estimated that, under intense fishing pressure in the early 1960’s in southern Georgian Bay (Lake Huron), the fishery removed, in successive years, 68 and 61% of all whitefish between ages VI and VII. They also estimated that the natural mortality rate in the absence of fishing would have been only about 34%.

After the 1947-49 peak, abundance declined until extremely low levels of production of the late 1950’s were reached. Possibly the substantial increase in the smelt population was a contributing factor; the alewife apparently was not, however, since the whitefish had become scarce before the alewife could have caused any effect. Sea lamprey predation assuredly contributed to this decrease, but perhaps not greatly in the beginning. The very high incidence of lamprey wounds on the lake trout in the 1940’s, and its rapid extermination, leave little doubt that so long as the lake trout was available it was the favorite mark of the sea lamprey. Although whitefish was attacked by the lamprey soon after the predator's penetration into Lake Michigan (Shetter 1949), it probably did not suffer greatly until the lamprey had destroyed the lake trout populations and needed to turn elsewhere for prey. After the lake trout's collapse, however, whitefish may have been victimized extensively. Roelofs (1958) believed that a high (94%) mortality rate in whitefish of Big Bay de Noc (in northern Green Bay) between ages III and IV in the period 1951-54, may have been due to sea lamprey attacks, because local commercial fishermen reported that frequently large numbers of dead, commercial-sized whitefish, showing a high incidence of lamprey scarring, drifted into their nets. Spangler (1970) concluded that sea lamprey predation was an important component of natural mortality of whitefish in northern Lake Huron, because seasonal fluctuation in mortality of whitefish was positively correlated with seasonal changes in the incidence of lamprey scarring.

We attribute the increase of whitefish in the 1960's primarily to the lessened sea lamprey predation. Lower predation resulted mostly from sea lamprey control efforts, but probably also to some degree from the lake trout restocking program, which has restored to the predator its more favored victim. Recent work in northern Lake Huron has shown that the scarring rate on whitefish is influenced not only by the abundance of the sea lamprey, but also by the abundance of other prey species, e.g., the white sucker (Anonymous 1969).

Lake trout

The lake trout was the most valuable commercial species in Lake Michigan from 1890 until the mid-1940's. Production in Lake Michigan was usually the highest of any of the Great Lakes in that period.

Relatively few lake trout were caught in the earliest days of the fishery because they were not highly esteemed as long as whitefish were plentiful (Koelz 1926). In 1879, the first year for which records are available, production was a relatively low 2.6 million pounds; production then increased rapidly to 6.4 million pounds in 1885 (Fig. 7). Beginning in 1890 the fishery was characterized by exceptional stability for several decades, but some trends (mostly downward) were evident. A thorough treatment of these fluctuations by Hile, Eschmeyer, and Lunger (1951) is summarized briefly here. In 1890-1911 the catch was rather consistently high, averaging 8.2 million pounds. The average annual yield then dropped to 7.0 million pounds in 1912-26, and declined further to 5.3 million pounds in 1927-39. The trend was reversed in 1940-44 when the catch was above 6 million pounds in every year, and the average was 6.6 million. The year 1945 marked the beginning of a precipitous decline that led to a catch of only 342,000 pounds in 1949 and a mere 34 pounds in 1954. Lake trout were extremely rare in 1955 (Eschmeyer 1957) and the species probably became extinct in the lake in 1956.

Declines in lake trout stocks were observed in certain areas of Lake Michigan even before the 1880's, when production first became high (Milner 1874; Smith and Snell 1891). Since the declines were accompanied by appreciable decreases in average size, they probably were the result of

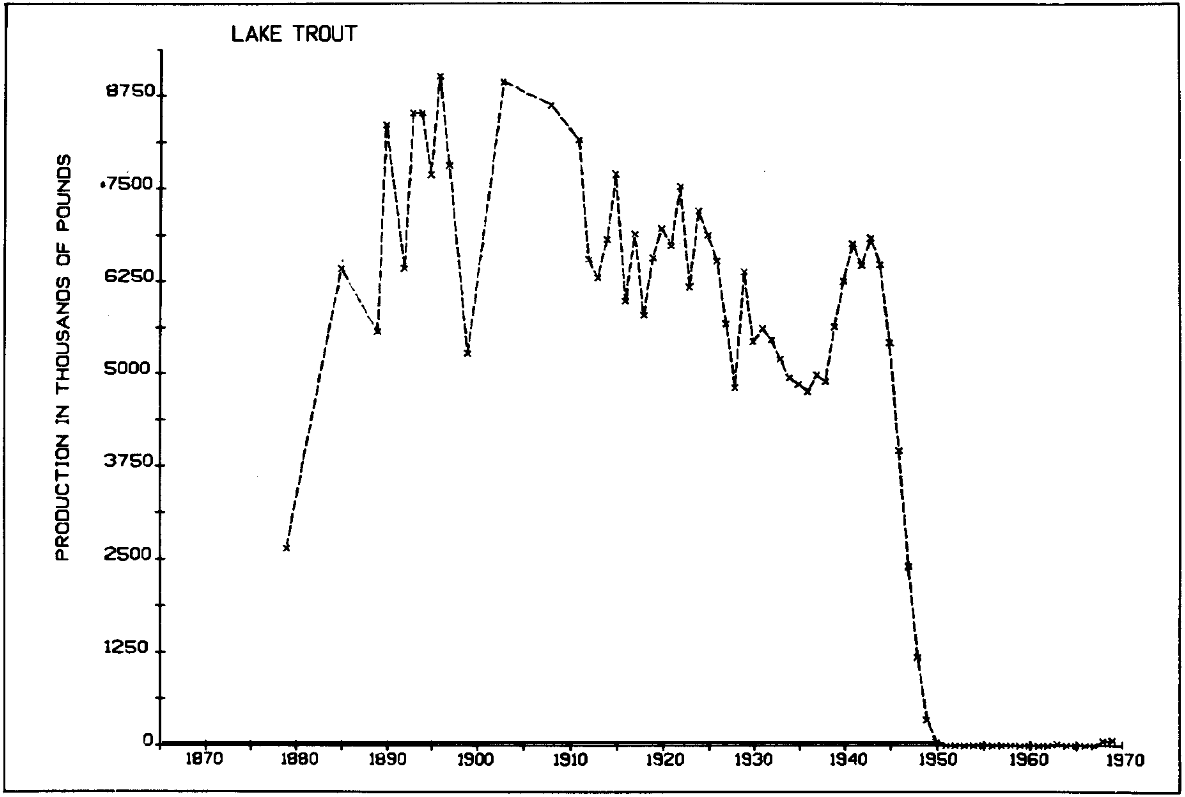

Figure 7. Commercial production of lake trout in Lake Michigan, 1879-1970.

exploitation. It is doubtful that this decline was lakewide, however, although a general decline in the stocks began shortly thereafter. Van Oosten (1949) noted that the gradual decrease in production during 1893-1938 occurred in the face of greatly increased fishing intensity. He believed that the decline was due to excessive exploitation, and we concur in that belief.

That the sea lamprey had a powerful influence on the phenomenal decline of the lake trout in Lake Michigan after 1944 is beyond question. Some authors held the sea lamprey totally responsible (Hile, Eschmeyer, and Lunger 195 1; Eschmeyer 1957). Smith (1968) however, speculated that although sea lamprey predation hastened the decline once it had begun, the decline was initiated by markedly increased lake trout exploitation in Illinois waters in 1940-44. Although we agree with Smith that the increased lake trout yields of 1940-44 (275% above 1927-39 average) in Illinois were disproportionate to any likely increase in abundance, we question that an increase in production (and probably decrease in stocks) in so small an area in the southwest corner of Lake Michigan (Illinois waters are only 7% of total) could have exerted such an abrupt influence on stocks throughout the entire lake. Such an occurrence would have required extremely rapid dispersion of lake trout. The best evidence is that, although some lake trout in Lake Michigan travel widely, general dispersion is slow (Smith and Van Oosten 1940; Great Lakes Fishery Commission 1970). We believe that the disappearance of lake trout in Lake Michigan was a direct result of sea lamprey predation, although the lake trout was being somewhat overexploited before the parasite appeared. Whether a less exploited population could have better withstood the lamprey's assault is questionable, although that must be considered a possibility.

As a result of stocking, lake trout are once again abundant in Lake Michigan. Small experimental plants (36,000 to 94,000, mostly yearlings) were made each year in 1959-62 for a variety of studies relating to behavior of the stocked lake trout and their age before being subjected to heavy sea lamprey predation (Robert Saalfeld, personal communication). Rehabilitation was not an objective in these experimental plantings, since effective sea lamprey control had not yet begun. These trout apparently had disappeared by 1964.

The rehabilitation program, coordinated by the Great Lakes Fishery Commission, began in 1965. Since then an average of nearly 2 million yearling lake trout (average length about 6 inches) have been stocked each year. The program to date has been highly successful in producing fish to spawning size, in spite of continued troublesome sea lamprey predation. The trout have grown rapidly, attaining an average weight of about 4 pounds after only 3 years in the lake. Although spawning is known to have occurred in 1969 and 1970, no young have as yet been observed. Commercial fishing is prohibited, but a rapidly expanding sport fishery took more than 1 million pounds of lake trout in State of Michigan waters alone in 1970 (unpublished data, Michigan Department of Natural Resources).

Deepwater ciscoes

The deepwater ciscoes in Lake Michigan have supported a commercial fishery since at least 1869 (Koelz 1926). Reasonably complete commercial production records, however, have been kept only since 1926. Before then deepwater cisco catches were often either combined with other species (e.g., whitefish) in the statistics or not recorded at all (Hile and Buettner 1955). Even since 1926 the statistics for deepwater ciscoes have not been separated by species-all have been grouped as "chubs." The seven species originally represented (in order of decreasing size) were: *Coregonus nigripinnis, C johannae, C zenithicus, C. alpenae, C. reighardi,* C *kiyi,* and C. *hoyi.* In the following discussion most of these species are referred to by scientific name, since that is the usual practice. Exceptions are the blackfin *(C. nigripinnis)* and the bloater (C *hoyi),* which are well known by their common names.

Although the early records are not accurate, it may be inferred from the statistics that annual deepwater cisco production (Fig. 8) often amounted to several million pounds between the early 1890's and 1925 (Hile and Buettner 1955). The catches averaged 4.6 million pounds and were rather stable in 1926-39, dropped abruptly to 1.6 million pounds in 1940, remained near that figure through 1942, and then increased steadily to 9.3 million pounds by the end of the decade. The catch in the 1950's was nearly constant and averaged 10.2 million pounds. Peak annual production was in 1960-62 (12.0 million pounds). Landings dropped sharply to 7.5 million pounds in 1963 and 5.2 million pounds in 1964, but then began a steady increase to 10.1 million pounds in 1968 and were at 9.5 million pounds in 1970.

Trends in commercial production (even when based on catch per unit of effort) are not wholly satisfactory indicators of changes in abundance of deepwater ciscoes. Although the same is true to some extent for all the commercial species in Lake Michigan, the problem is much more acute for deepwater ciscoes for a variety of reasons, as described below:

Changes in fishing gear-particularly in mesh size-have been exceptionally great for deepwater ciscoes. The earliest gill nets for catching these species were of mesh sizes as large as 4½ inches, stretched measure (Smith and Snell 1891), but by 1950 the mesh size most commonly used had decreased to 2½ inches, and by the end of the decade 2-3/8-inch mesh was permitted in some areas (Smith 1964). The netting material changed, beginning about 1929, from linen to more efficient flexible cotton nets, and then changed again in 1946-52 to much more efficient nylon nets (Hile and Buettner 1955). A limited otter trawl fishery took great quantities of deepwater ciscoes (mostly small) in 1960-62. Differences over the years in the proportion of the catch sold by the fishermen have also influenced production without regard to abundance. Through most of the early history of the fishery small ciscoes usually were discarded (Moffett 1957), but in later years most were sold.

Perhaps the greatest shortcoming of the production records as indicators of changes in deepwater cisco populations has been a general lack of separation by species (except to some extent for the blackfin and *C johannae* in the early fishery). Periodic systematic experimental fishing, however, has provided a clear picture of changes in the last four decades. The first survey was in 1930-32, when the U.S. Bureau of Fisheries R/V *Fulmar* fished linen gill nets extensively in Lake Michigan. The U.S. Fish and Wildlife Service R/V cisco repeated much of *the Fulmar* sampling (identical gear, seasons, and locations) in 1954-55 and again in 1960-61 (for descriptions of the surveys, see Moffett 1957 and Smith 1964). Since 1961 the cisco has monitored Lake

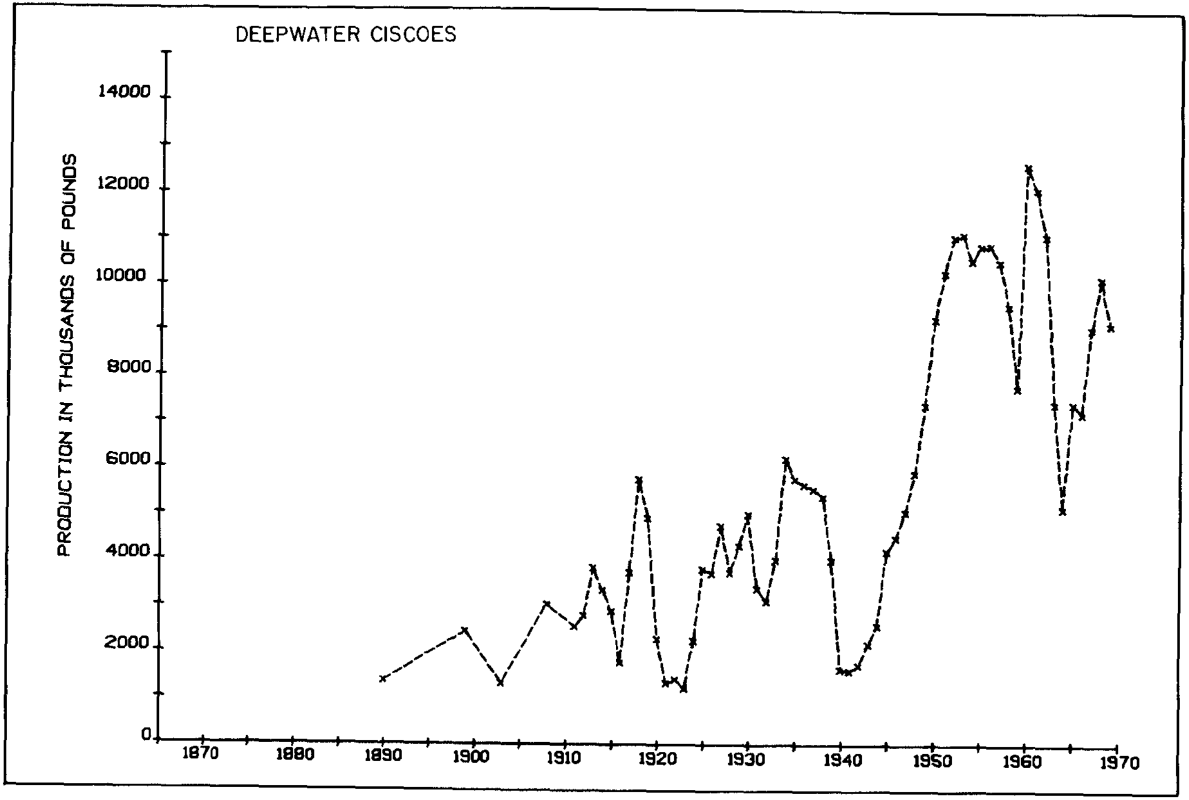

Figure 8. Commercial production of deepwater ciscoes in Lake Michigan, 1890-1970.

Michigan stocks of ciscoes (as well as other species) each year, particularly in the southern portion of the lake. Most of the recent sampling has been with trawls.

Changes in deepwater cisco stocks up to 1960-61, based mostly on the three surveys described above, were documented in considerable detail by Smith (1964). A brief summary of these changes is presented here. The largest species, the blackfin and *C johannae,* which supported the earliest fisheries (on the basis of inferences from the sketchy early records), made up only a small portion of the population in 1930-32; both apparently became extinct in the 1950's. Four others-C *zenithicus, C alpenae, C reighardi,* and C kiyi-declined sharply in abundance between 1930-32 and 1960-61. The numbers of bloaters, the smallest of the ciscoes, increased several-fold between 1930-32 and 1954-55; abundance changes between 1954-55 and 1960-61 are in doubt, since some areas showed increases, others decreases. The percentage of bloaters in experimental catches of deepwater ciscoes increased from 31 in 1930-32 to 76 in 1954-55 and almost 94 in 1960-61. Although the average size of each species decreased between 1930-32 and 1954-55, no further decrease was evident by 1960-61. Rather, the average length of bloaters in experiment trawl catches increased noticeably between 1954 and 1960 in southern Lake Michigan (Brown 1970).

The causes for the described changes (up to the early 1960's) in abundance of deepwater ciscoes in Lake Michigan are several. It seems almost certain that the large blackfin and *C johannae* were simply over-exploited in the early fishery, since they had become scarce before an effect on these deepwater species by any other factors would have been likely. Inferences from Koelz (1926) indicate that the intermediate-sized deepwater ciscoes were depleted to a considerable extent through overfishing by the 1920's. Reasons for changes in deepwater ciscoes in later years are more complex. Data in the following paragraph are from Smith (1968), and apply to changes from the early 1940's to the early 1960's.

Low production in the early 1940's was a result of reduced effort rather than low abundance. As the lake trout declined in the late 1940's and early 1950's, fishermen shifted to deepwater ciscoes and production increased greatly. During the same period predation on the deepwater ciscoes by sea lampreys became increasingly severe, as the lamprey's favored deepwater prey, the lake trout and burbot, disappeared. Both the fishermen and the lampreys selected the larger cisco species, thereby favoring the bloater. The bloater also benefited from the termination of predation by the lake trout, for which it had been a primary food. The result of these events was the previously described situation in the early 1960's: the largest deepwater ciscoes (blackfin and *C johannae)* apparently had been exterminated; the intermediate-sized species (C. *zenithicus, C alpenae, C reighardi,* and C *kiyi)* were uncommon; and the smallest (blaoter) was very abundant.

Rapid changes in deepwater cisco populations have continued since 1960-6 1. The bloater has become even more dominant; it made up more than 99% of the deepwater ciscoes taken in experimental trawls in 1964 (Wells 1966). By 1969 only a rare *C. reighardi* or C. *kiyi* was caught in experimental nets; even these few "non-bloaters" were not as distinct morphologically as formerly, their appearance suggesting hybridization with the bloater (see

Smith 1964 for a discussion of possible cisco hybridization in Lake Michigan). *C. alpenae* and *C zenithicus* apparently were extinct, or virtually so, in 1969, at least in the southern portion of Lake Michigan. Since the bloater dominated the deepwater cisco stocks so completely after 1960-61, further remarks here refer to that species only.

The abundance of bloaters decreased in Lake Michigan after 1960-61. Average catches per lo-minute trawl tow in identical series in southeastern Lake Michigan in late October or early November 1963-70 were 37, 33, 30, 16, 18, 25, 12, and 15 in the successive years. As abundance declined, size increased. Brown (1970), in fact, showed that, on the basis of experimental trawl catches, the average length of bloaters increased gradually throughout the period 1954-69, from 174 mm to 249 mm. Much of the increase to the early 1960's was due to faster growth, but in recent years the increase has been due mostly to a greater proportion of older fish in the population; the average age increased from 3.5 years in 1964 to 6.0 years in 1969 (Brown 1970). Poor recruitment and a lowered mortality rate among older fish appear to be responsible.

The decrease in numbers of bloaters in recent years probably has been at least to a large degree offset, in terms of biomass, by the significant increase in average weight of the fish (in Lake Michigan, bloaters nearly double in weight in growing from 213 to 249 mm, the average lengths in 1964 and 1968). This increase in weight, plus the greater vulnerability of large bloaters to commercial gill nets, was largely the reason for the increase in commercial production that began in 1965 (commercial trawling for ciscoes was unimportant by this time), in spite of a reduction in numbers of fish in the stocks. Also partly responsible for the gain was the increase in fishing intensity that followed a reduction in 1963-64. (The reduction had resulted from a marked decrease in demand after several persons who had eaten smoked ciscoes from Lake Michigan died of botulism poisoning.)

The increased growth rate of the bloater in Lake Michigan may have been a response to decreased intraspecific competition as numbers declined. The environmental factor or factors leading to poor recruitment, which was the main cause of this decline, are not clear. The alewife, however, is an obvious suspect. During its explosive increase in Lake Michigan from the 1950's to early 1967, it must have become increasingly competitive with the bloater. In the previously described alteration of zooplankton population by alewives between 1954 and 1966, large zooplankton species and zooplankton biomass were much reduced. Since young bloaters up to a length of several inches feed almost exclusively on zooplankton (Wells and Beeton 1963), the implications are obvious. Alewives also may be detrimental to bloaters by feeding on their eggs. Lake Michigan bloaters spawn in January-March, mostly at depths of 40-60 fathoms (73-1 10 m), at a time and place of great alewife concentrations (Wells 1966). Alewives are known to include fish eggs in their diet in Lake Michigan (Morsell and Norden 1968; unpublished data of Great Lakes Fishery Laboratory).

The apparent decrease of mortality among the older bloaters in recent years is probably due to lessened sea lamprey predation. Although sea lamprey control in Lake Michigan began in 1960 it was probably not until about 1966, when all lamprey producing tributary streams had been treated with lamprey larvicide, that the lamprey population had been reduced greatly. Intensive lake trout stocking, which began in 1965, also gave the sea lamprey an alternate, more favored victim, but perhaps not until about 1968, when substantial numbers of lake trout had grown to a size preferred by the lamprey.

The outcome of the recent rapid changes in bloater stocks is a subject of some concern. In addition to increased growth since the mid-1950's, and decline in numbers which began about that time (Brown 1970) or a few years later (Smith 1968) a marked shift in sex ratio also has occurred. The percentage of females in the population rose from 75 in 1954 to 97 in 1961, then changed little through 1967 (Brown 1970). Smith (1968) and Brown (1970) interpreted these changes as a response to environmental stress that probably will culminate in a disastrous decline in the stocks. Both authors based their views on similar changes which preceded sharp declines in other Coregonid populations (e.g., lake herring in Birch Lake, Michigan). Remarks by commercial fishermen have indicated that the average size of ciscoes also became very large just before their drastic reduction in the middle and late 1960's in Lake Huron.

In 1968, 1969, and especially in 1970, young-of-the-year and yearling bloaters appeared in experimental catches in far greater numbers than in any years of experimental fishing since 1955 (1960-71). The success of these young follows the severe reduction in alewife abundance after the spring of 1967 and the subsequent shift in zooplankton populations back toward 1954 levels (Wells 1970). It is of course too early to predict whether this recent success (and an accompanying increase in the proportion of males in the population) represents the beginning of a recovery of bloater stocks in Lake Michigan.

Lake herring

Lake herring production often was the highest of any species in the early fishery of Lake Michigan. In 1890, the first year for which figures were recorded, 6.1 million pounds were landed (Fig. 9). Production increased rapidly after 1890 and was very high in 1893-1908. Actual figures for this period are available for only 1899, 1903, and 1908, when 22.2, 15.4, and 24.2 million pounds, respectively, were recorded, but annual catches of 20.1-25.9 million pounds of lake herring and deepwater ciscoes combined in the other years were almost certainly mostly lake herring. Production dropped shortly thereafter, and has never returned to such high levels. The average annual catch was about 9.0 million pounds in 1911-18 and about 4.5 million pounds in 1919-38. Production dropped further to an average of only 1.6 million pounds in 1941-44, increased rather strikingly to 9.7 million pounds in 1952, and then declined to an average of only about 40,000 pounds per year in 1963-70. Green Bay has contributed about 87% of the lake herring catch of Lake Michigan since 1936 when, according to Smith (1956), reliable records of Green Bay's portion of the catch were first available.

Wide fluctuations in production of lake herring have been characteristic of all the Great Lakes. Although changing market demand for this generally low-value fish has influenced production, the primary reason for the great differences in catch unquestionably has been changes in abundance. The

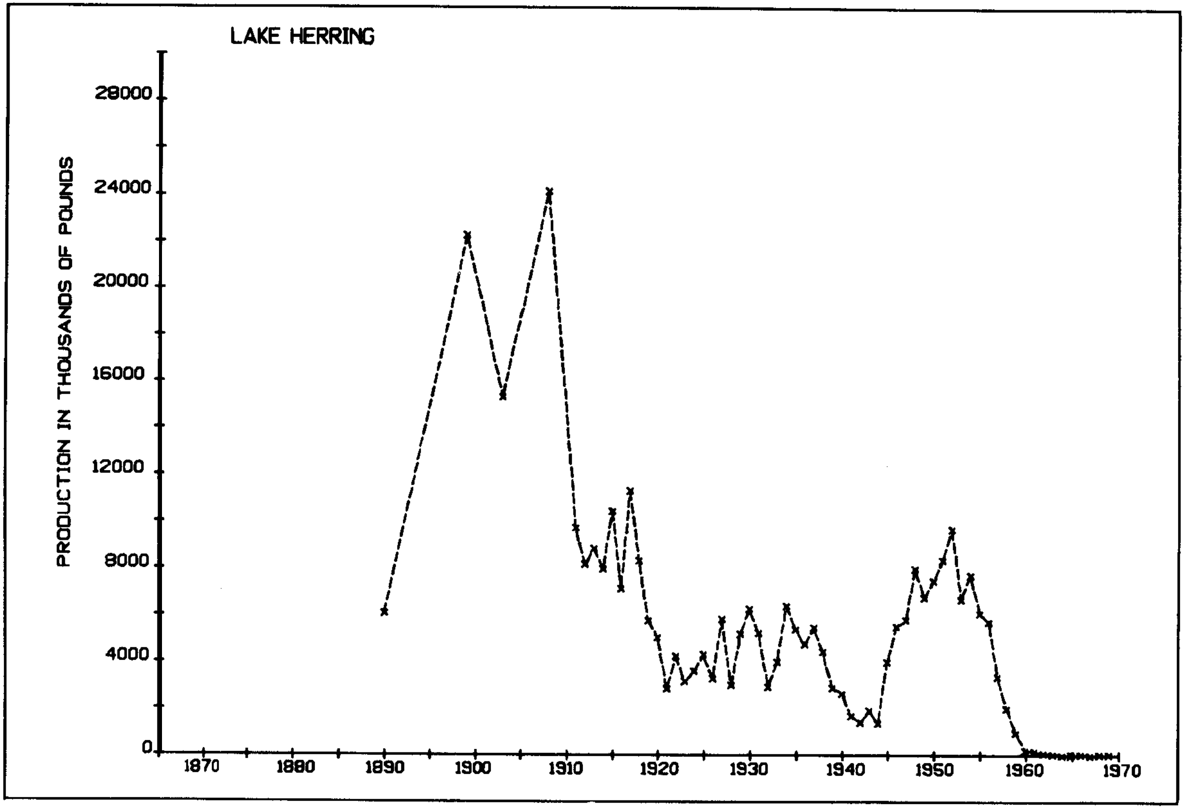

Figure 9. Commercial production of lake herring in Lake Michigan, 1890-1970.

general trend in production has been downward, although exceptionally strong year classes, e.g., the 1944 year class in Lake Erie (Scott 1951), occasionally have caused spectacular increases in the catch. Lake herring are far less abundant now than formerly in all the Great Lakes, The declines have been attributed to various causes: overfishing in Lake Erie (Van Oosten 1930); the influence of smelt and (to a smaller degree) bloaters in Lake Superior (Anderson 1969); and the effects of alewives in Lake Michigan (Smith 1970).

The early marked declines of lake herring in Lake Michigan were largely the result of heavy exploitation, although pollution must have been detrimental in southern Green Bay. The further decline (in the 1920's and 1930's) would seem also to relate to exploitation, but smelt probably were adversely affecting lake herring during the 1930's. The decrease of lake herring abundance which began in 1939 and resulted in an average production of only 1.6 million pounds in 1941-44, and the subsequent striking increase after the catastrophic smelt dieoff of 1942-43, suggest strong influence by the smelt. (Although over 2 million pounds of smelt were produced in Lake Michigan in 1943, nearly all were taken in winter before the dieoff had ended-only 5,000 pounds were caught in 1944.) The greatly reduced numbers of smelt in the spring of 1943 probably allowed a strong year class of lake herring to develop (through decreased competition for planktonic food with lake herring fry, or less predation on them, or both) as indicated by a much improved commercial catch in 1945. Production figures indicate that relatively strong year classes continued until the early 1950's, since the disastrous decline which has carried to the present did not begin until 1957. It seems likely that the resurgence of smelt to considerable abundance by the early 1950's, in combination with the explosive increase of alewives which began in the mid-1950's, has reduced the lake herring to its present insignificance in Lake Michigan.

Lake sturgeon

The lake sturgeon was reduced in abundance more abruptly than any other species in the early commercial fishery of Lake Michigan. Numbers had decreased in many areas before 1879 (Smith and Snell 1891), the year of first production records. The catch dropped from 3.8 million pounds in 1879 to only 96,000 pounds in 1899 (Fig. 10). A decline in catch to only 2,000 pounds in 1928 led to the complete protection of sturgeon from exploitation in Lake Michigan the following year. The closure was probably of little consequence, however. Sturgeon were so scarce for several years before 1929 that it is unlikely that fishermen sought them; nearly all catches must have been incidental. The incidental catch surely continued after the closure, and it is doubtful that many sturgeon thus caught were returned to the lake alive. Sturgeon fishing was legalized again in State of Michigan waters in 1951, but the annual catch since then has never exceeded 5,000 pounds.

The disastrous decline of the lake sturgeon was primarily a result of overfishing, although stream degradation probably was detrimental to spawning areas in rivers and near river mouths. Before about 1875 the commercial fishermen attempted purposely to exterminate the lake sturgeon because it damaged nets and otherwise interfered with fishing for other species, and because it had no commercial value. It was commonly removed from the nets

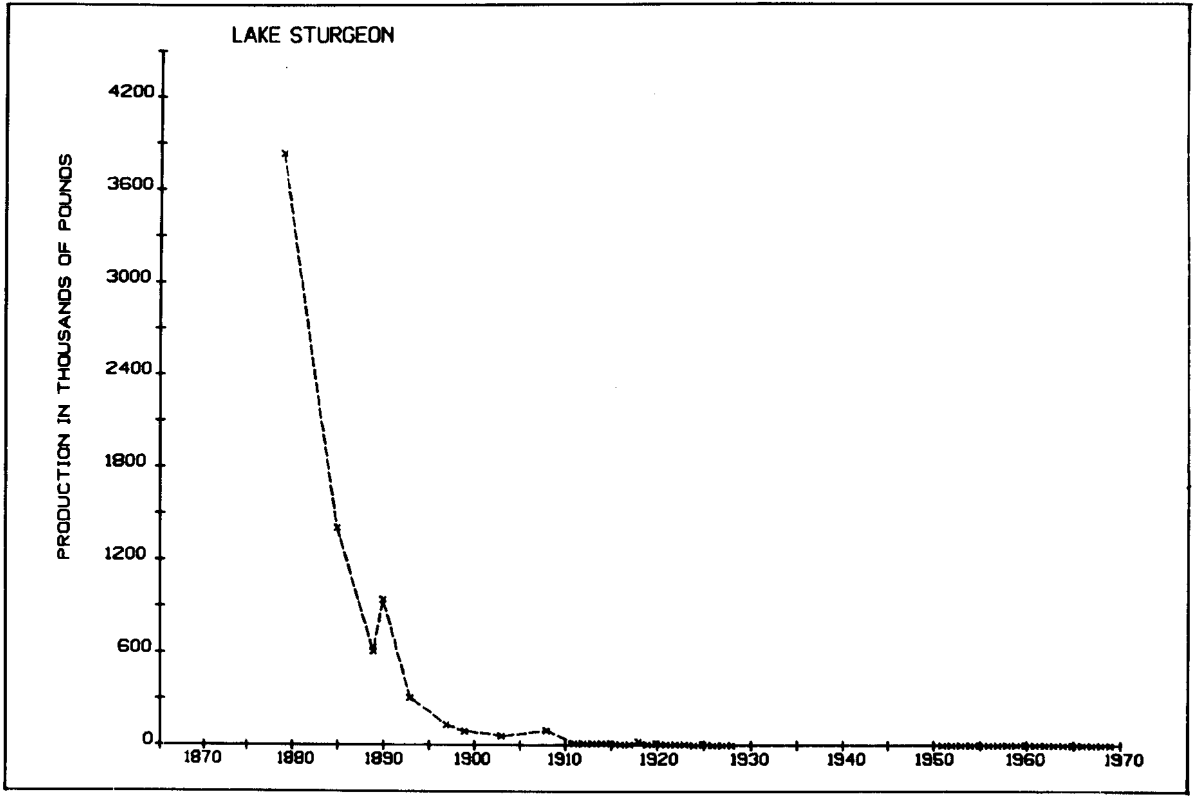

Figure 10. Commercial production of lake sturgeon in Lake Michigan, 1879-1970 (protected from commercial fishing 1929-1950).

in huge numbers and thrown into offal heaps on shore (Milner 1874), or fatally wounded and returned to the lake (Koelz 1926). Later, however, the lake sturgeon became valuable for its flesh, eggs (caviar), oil, and air bladder (for the manufacture of isinglass). The sturgeon's prolonged period of immaturity (about 22 years for females-Van Oosten 1956) reduced its chances of escaping nets long enough to reach spawning age and probably precluded any possibility that it could have maintained high populations in the face of the heavy fishing to which it was subjected, even if stream degradation had not occurred.

Yellow perch

Yellow perch have supported important sport and commercial fisheries in Lake Michigan. Although sport catch statistics are not available, the take must have been considerable until the last decade because breakwalls around the lake often were lined with dozens of successful anglers.

Commercial production has averaged 2.4 million pounds annually from 1889 (when records began) through 1970. Three notable deviations from this average have occurred: in 1894-96, when the average was 6.3 million pounds; in 1961-64, when the take averaged 4.9 million pounds; and in 196570, when production dropped abruptly to an average of only 890,000 pounds (Fig. 11). Southern Green Bay usually has been a particularly heavy producer of yellow perch, although all shallow areas of the lake have yielded this species in commercial quantities.

Yellow perch apparently were not abundant in the earliest days of the fishery. Smith and Snell (1891) reported that perch were uncommon in southern Green Bay before 1882, but increased spectacularly soon thereafter when whitefish and walleyes became rare. At about the same time perch also increased in extreme southern Lake Michigan, after a decline in whitefish and sturgeon.

The high yellow perch production of 1894-96 was probably related to high abundance and increased fishing effort as the species came into favor in the commercial trade. The production peak in the early 1960's was caused by increased fishing intensity and perhaps greater abundance; the sudden decrease in catch which followed obviously resulted from a much reduced abundance, as indicated by catches in experimental trawls.

The recent trends in yellow perch populations undoubtedly were related to alewife abundance. The increased production and subsequent decline of perch in the 1960's did not occur in all portions of the lake simultaneously but progressed from north to south, just as did the increase in alewife abundance. Peak production in the northern part of Lake Michigan (except Green Bay) was in 1960 (unpublished commercial fishery records by statistical districts compiled by the U.S. Fish and Wildlife Service). Production in Green Bay held at a high level in 1960-63. Production in the southern portion of the lake was highest in 1963-64; by that time the species had become scarce in the northern part. The increase and subsequent abrupt decline progressed southward somewhat more rapidly on the west side of the lake than on the east side. Abundance in Green Bay and the extreme southeastern portion of the lake never reached levels as low as those in other parts.

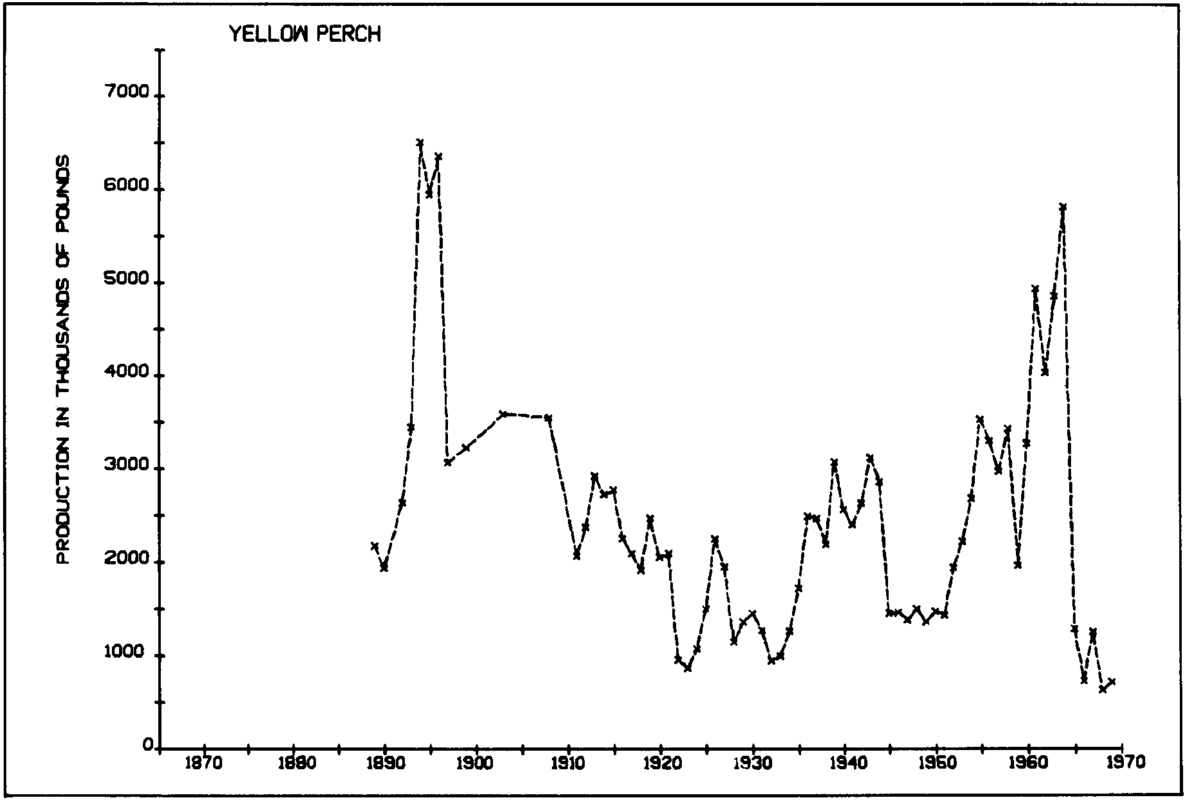

Figure 11. Commercial production of yellow perch in Lake Michigan, 1889-1970.

The alewife's primary damage to yellow perch seems to be in inhibiting reproduction. Lack of recruitment in the early and middle 1960's (a period when young perch were seldom taken in experimental catches of the R/V Cisco) led to the drastic decline (which no doubt was hastened by heavy exploitation). Evidence that the alewife may have been responsible for the poor hatches is provided by the exceptionally strong year class that developed in southeastern Lake Michigan in 1969, after the decline of alewives in 1967 and 1968. Perch in Lake Michigan spawn in shallow areas in spring when alewives also are concentrated inshore. No perch eggs have been found, however, in stomachs of alewives taken on several occasions from among spawning perch in southeastern Lake Michigan (unpublished records of Great Lakes Fishery Laboratory). Perhaps the gelatinous matrix in which perch eggs are embedded provides protection against predation by alewives. If so, it then seems likely that alewives adversely affect reproduction of perch by competing with, or feeding on, the fry.

The reason for the increased production (and catches per unit of effort) immediately before the drastic decline of the 1960's is not certain. Unfortunately the perch in the commercial catch were not examined, and systematic experimental fishing for perch was not conducted before peak production. Commercial fishermen indicate, however, that perch in the catches during peak production in southern Lake Michigan were larger than formerly, suggesting that the poorer reproduction of perch may have resulted in faster growth of those which survived-as occurred among deepwater ciscoes in the early 1960's (Brown 1970). The higher perch production per unit of effort may therefore have been a result of the capture of larger fish, rather than greater numbers. On the other hand, perhaps there was an increase in numbers of market-sized fish before alewives became extremely abundant, as asserted by Smith (1970) who attributed the increase to a greater supply of food provided by young alewives.

Walleye

The walleye has not generally been of great importance in Lake Michigan, having usually been taken incidentally with other species in the commercial catch. In one period (late 1940's to mid-1950's), however, it was vigorously sought by commercial fishermen and at the same time attracted great numbers of sport fishermen. Commercial production was 7 12,000 pounds in 1893, the only year before 1899 in which walleyes were recorded separately (Fig. 12). The average catch of 623,000 pounds in other years before 1899 included northern pike and saugers (Stizostedion canadense) although most probably were walleyes. From 1899 to 1946 production ranged between 31,000 and 345,000 pounds (average 128,000 pounds). A pronounced increase after 1946 to 1.3 million pounds in 1950 was followed by a decrease to 301,000 pounds in 1952 and another peak of 976,000 pounds in 1955. A steady decline after 1955 brought production to only 12,000 pounds in 1970.

The Lake Michigan walleye fishery is centered in Green Bay, which produced an average of 96% of the total annual catch in 1947-70. Production usually has been concentrated in the northern portion of the bay since 1930,

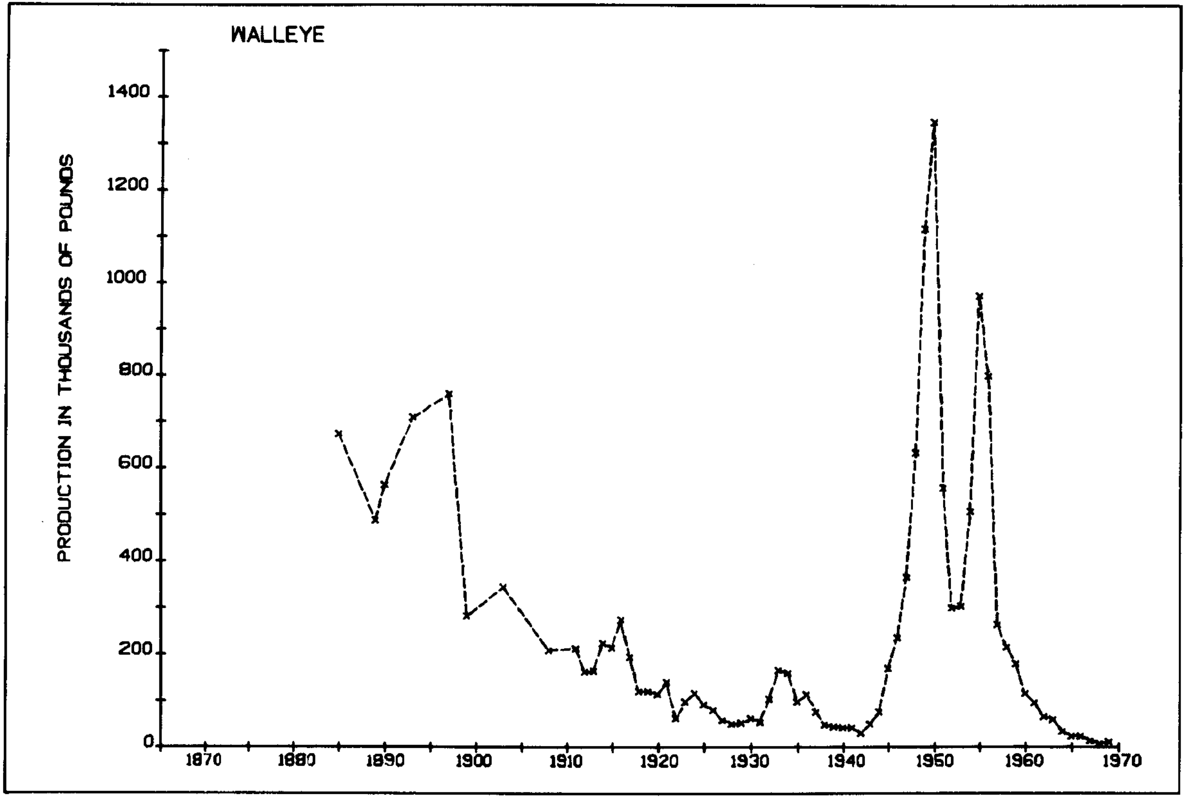

Figure 12. Commercial production of walleye in Lake Michigan, 1893-1970.

but was often greatest in the southern part before that time. Walleyes caught in the main body of Lake Michigan have come mainly from the east shore between Frankfort, Michigan, and the Michigan-Indiana border.

Although trends in abundance have not always been indicated by records of walleye production (Hile, Lunger, and Buettner 1953; Pycha 1961), certain broad changes are clearly apparent: Abundance declined substantially in southern Green Bay early in the fishery and has been generally low there since 1930; it reached peaks in northern Green Bay in 1949-50 and again in 1955-56 (Pycha 1961); and it has declined so greatly since 1956 that the species is not now common in any part of the lake.

Reasons for the early decline in walleye abundance in southern Green Bay are not clear. The severe decrease of walleyes which occurred there (coincidentally with a decrease in whitefish) before 1882 (Smith and Snell, 1891) probably was the combined result of heavy fishing and deteriorating environment; the generally low abundance since 1930 might logically be blamed on the unsuitable habitat in that heavily polluted area. The abundance peak in northern Green Bay in 1949-50 resulted from an extremely strong 1943 year class, which made up 57% of the catch even as late as 1952 (Pycha 1961). The high abundance in 1955-56 was the result of strong year classes in 1950, 1951, and 1952, the strengths of which approached or exceeded that of 1943 (Pycha 1961). These large year classes never carried commercial production as high as did the single 1943 year class, however, because, according to Pycha (1961), an intensive sport fishery cropped a large portion of the fish at a relatively small size.

The decline in walleyes since the mid-1950's seems too persistent to involve simply a chance succession of poor year classes. The eastern Lake Michigan stocks as well as those of Green Bay are now at extremely low levels. The reasons are not at all obvious. Fishing pressure, at least in eastern Lake Michigan, has decreased considerably in the past decade in the shallow areas inhabited by walleyes. Pollution in some streams is possibly inhibiting reproduction, but some of the best spawning streams-e.g., the Whitefish River which flows into northern Green Bay (Crowe, Karvelis, and Joeris 1963) and the Muskegon River which flows into eastern Lake Michigan (Eschmeyer 1950; Eschmeyer and Crowe 1955) - do not appear to be unduly polluted now. Some larger streams along the east shore (e.g., the Kalamazoo River, which enters Lake Michigan at Saugatuck) are now badly polluted, but none of the east shore streams except the Muskegon River have had significant walleye spawning for at least several decades (Walter Crowe, personal communication).

Sea lamprey predation offers a possible explanation for the present poor state of the walleye stocks in Lake Michigan, but the relation is certainly not as conspicuous as in some cases of destruction of fish stocks by sea lampreys. Hile and Buettner (1959) held the sea lamprey responsible for the decline of walleyes in Saginaw Bay of Lake Huron, but as was pointed out by Pycha (1961), the sequence of events was different there: The decline of the walleye was coincident with, or only slight behind, the reduction of the lake trout by lampreys, whereas in Lake Michigan walleyes were still abundant when the lake trout was finally exterminated. Lake trout (and perhaps other species) were, of course, preferred by sea lampreys, and perhaps the lamprey did not turn seriously to walleyes in Lake Michigan until the lake trout had become eliminated-but it is not clear why the same lag in predation effects would not have occurred in Lake Huron. It might be pertinent to mention that scarring rates on walleyes in Lake Michigan have always been low (Walter Crowe, personal communication) but probably this species, like the deepwater ciscoes, is almost always killed by a lamprey attack. (Deepwater ciscoes with a fresh lamprey wound and the lamprey which made the wound have occasionally been taken in trawls by the R/V *Cisco,* but no ciscoes bearing healed wounds have been caught.)

Alewives might have had an influence on walleye reproduction, but the relation is not obvious. If the walleye's decline has been a result of a long succession of year-class failures, the earliest failures would have to have occurred before 1955, on the basis of production records. Interference by the alewife at that early date is extremely unlikely. It is not too far-fetched to suppose, however, that the earliest year class failures were due to natural causes (e.g., weather conditions) and that by the late 1950's alewives were abundant enough to prevent any further possibility of a good hatch.

Suckers

Suckers have provided a moderately important commercial fishery in Lake Michigan. White suckers make up most of the catch, but longnose suckers and a few redhorse suckers (Moxostoma spp.) also are taken. Green Bay has been the center of production, but the northern portion of the main body of the lake yielded substantial catches several decades ago.

Commercial production of suckers in Lake Michigan ranged from 1.5 to 4.0 million pounds and averaged 2.1 million pounds in 1889-1949 (only 252,000 pounds were produced in 1885, the first year of record, and the only year recorded before 1889); no long-term trends developed in this period (Fig. 13). After 1949, production decreased, averaging only 766,000 pounds in 1950-60, and 337,000 pounds in 1961-68. An increase thereafter brought production to nearly a million pounds in 1970.

The production of suckers has been so strongly dependent on market demand that the catch figures are generally not useful as indices of abundance. It appears likely, however, that the severe drop in production which began in 1950 was at least partly due to decreased abundance resulting from sea lamprey predation. The sea lamprey has been shown to attack large suckers heavily in Lake Huron (Hall and Elliott 1954; Coble 1967), although it may not do so if more highly favored prey such as lake trout are abundant. The increase of sucker production in 1969-70 is perhaps related to decreased sea lamprey predation resulting from lamprey control and an increase in lake trout.

The abundance of suckers might have declined to some extent over the years, particularly in Green Bay, due to degradation of spawning streams.

Round whitefish

The round whitefish probably has never been abundant in Lake Michigan, except locally. Abundance is greater, however, than production figures

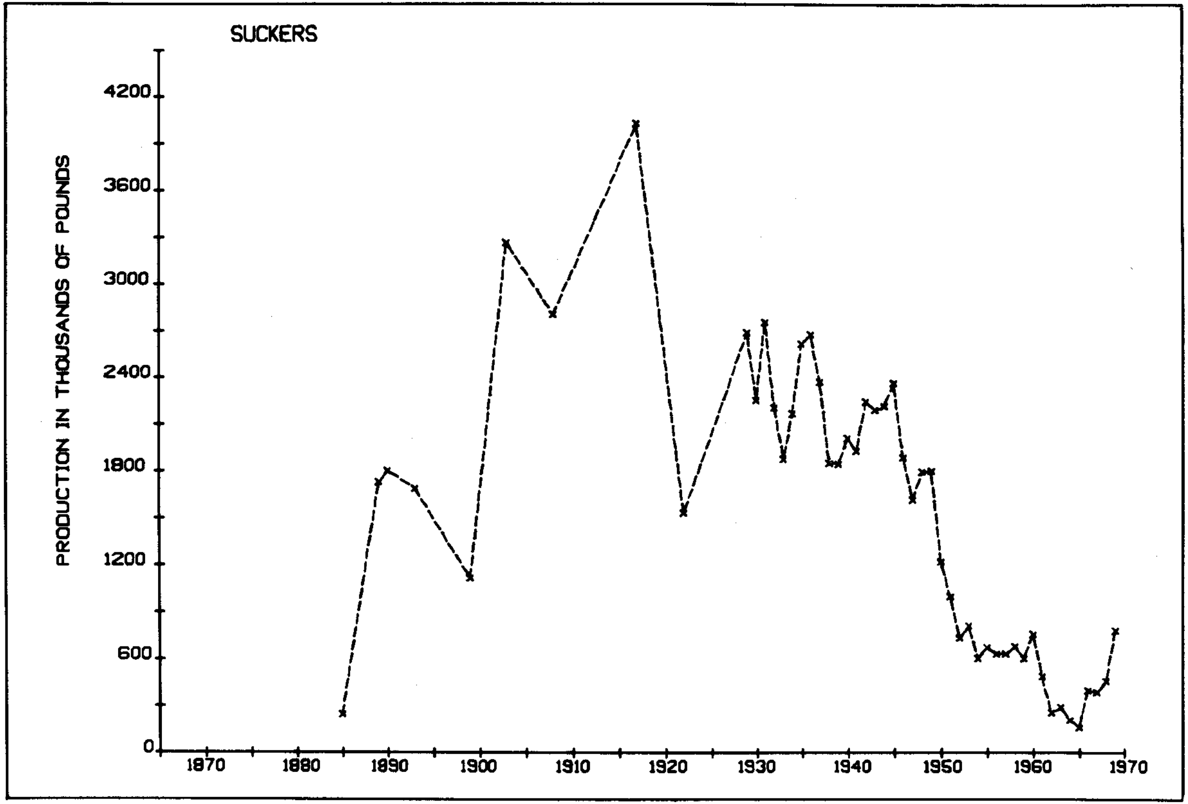

Figure 13. Commercial production of suckers in Lake Michigan, 1885-1970.

indicate because the round whitefish is usually sought only when the price is well above normal, or when fishing for more desirable species is poor. At other times much of the production is from incidental catches in nets fished for other species (e.g., lake whitefish).

Production of round whitefish was highest in the earliest years of record-423,000 pounds in 1893 and 519,000 pounds in 1899 (Fig. 14). The annual catch averaged 174,000 pounds in 1903-35, 57,000 in 1936-42, 126,000 in 1943-52, and only 19,000 in 1953-68. Production then jumped to 144,000 pounds in 1969 and 164,000 in 1970.

Although changes in production of round whitefish in Lake Michigan may not indicate abundance trends accurately (e.g., the substantially increased production in 1969 and 1970 was due mostly to increased effort by a few fishermen in response to improved prices), it is perhaps safe to speculate that the stocks have declined somewhat. Production in the late 1800's was considerably higher than that after 1900, and included (about 1885) catches of round whitefish "weighing 4 to 6 pounds each" (Smith and Snell 1891). Few approach that size today. Most commercial fishermen in the early 1940's thought that the round whitefish formerly had been more abundant (Gallagher and Van Oosten 1943). In the Muskegon-Grand Haven area of southeastern Lake Michigan, where production was 13,000 pounds in 1929 (the first year for which the catch was recorded by statistical districts), the species has rarely been seen since the late 1940's. The reasons for the apparent decrease are obscure.

Burbot

The burbot has never been of great commercial importance in Lake Michigan, owing to its low market demand. Even in the very early fishery burbot were discarded, except for a few sent to local markets (Milner 1874). Commercial production averaged 128,000 pounds annually for the 5 years of record in 1893-1917. The catch averaged 54,000 pounds in 1922-48 (no records for 1918-21) but dropped to only 13,000 in 1949-66. Production climbed to 61,000 pounds in 1967-70.

Since burbot have always been caught incidentally to other species and have been sold only as the small market demanded, production figures do not provide indices of abundance. From other sources (discussions with commercial fishermen and catches of the R/V *Fulmar* in 1930-32) it is evident that the burbot was once considerably more abundant than catch figures indicate. The three seasons of fishing with small-mesh nets by the *Fulmar,* for example, yielded about 6,000 burbot-or nearly one-half the total number of small lake trout caught (Van Oosten and Eschmeyer 1956). The burbot began declining at about the same time as the lake trout, however, and was reduced to rarity by the early 1960's; an increase, especially in Green Bay, reportedly began in the late 1960's.

The chronology of the changes in abundance of burbot in Lake Michigan in the past few decades strongly suggests that the sea lamprey was responsible for the decline, and that sea lamprey control led to the recent upswing in numbers.

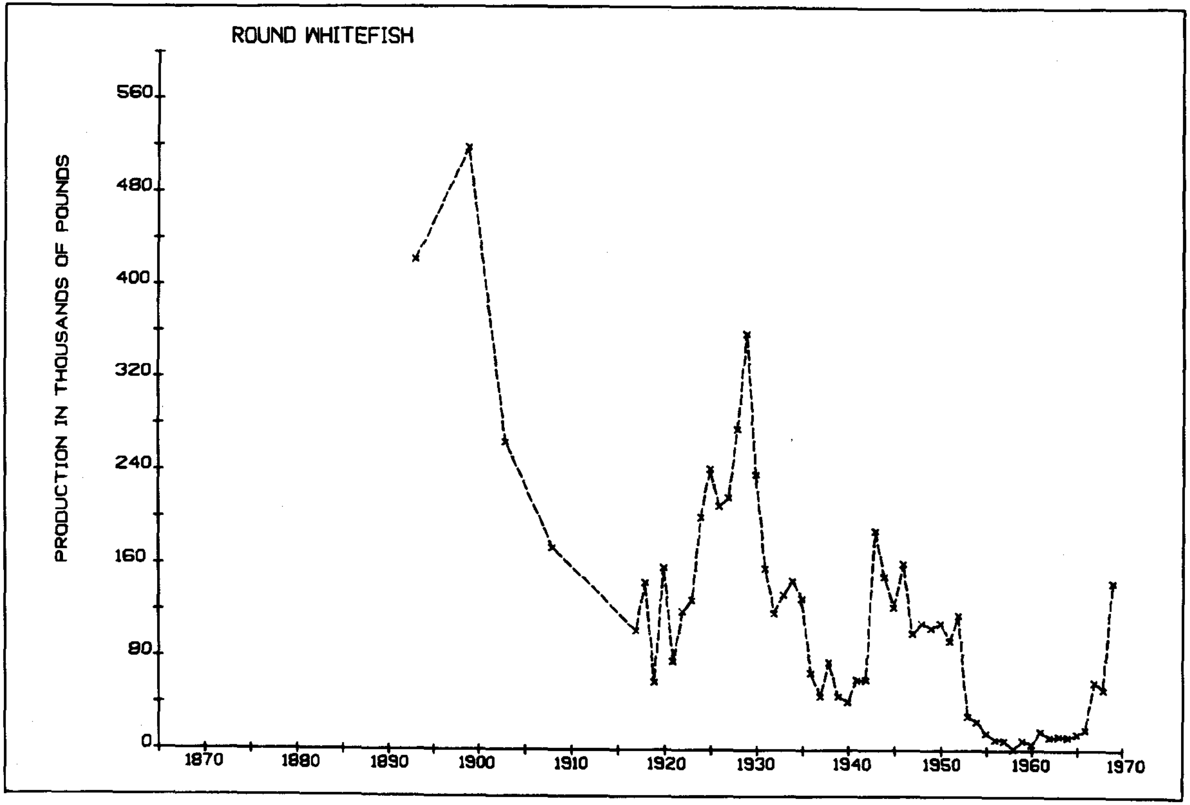

Figure 14. Commercial production of round whitefish in Lake Michigan, 1893-1970.

Emerald shiner

The emerald shiner has undergone perhaps the most extraordinary change in abundance of any species in Lake Michigan. Until about 1960, it was so abundant that it was regarded as a nuisance when it congregated in harbors in spring and fall. It occasionally clogged cooling water intake screens of power plants (Flittner 1964) and vessel engines (e.g., that of the *Cisco).* Statements by residents around Lake Michigan indicate that the emerald shiner once provided a substantial commercial fishery for the fish-bait market; no production records were kept, however.

The emerald shiner disappeared from Lake Michigan in the early 1960's, even though it had been abundant enough to cause a problem at a power plant in Milwaukee at least as late as November 1956 (Flittner 1964) and was still highly conspicuous in the harbor at Grand Haven, Michigan, in 1960 (personal observation of senior author). The last specimens taken by the R/V *Cisco* were off Saugatuck in 1962. A few were caught in the Kalamazoo River about 2 miles from its mouth in 1963 (Edsall 1964) suggesting that small resident populations (possibly geographical races) may remain in some tributary streams.

The extremely rapid disappearance of the emerald shiner concident with the population increase of the alewife leaves little doubt, as indicated by Smith (1970) that the two occurrences were related. The emerald shiner population certainly could not have been greatly affected by the existing levels of exploitation, and the almost simultaneous deterioration of its habitat over the entire lake is highly unlikely.

Information on the life history of emerald shiners in Lake Michigan is lacking, but inferences from studies in Lake Erie (Flittner 1964) indicate that the species fed mostly on zooplankton, so that it could have been destroyed due to an inability to compete for food with the alewife. The young emerald shiners, particularly, may have suffered in this respect. On the basis of studies in Lake Erie, emerald shiner eggs hatch in late spring and early summer (Flittner 1964) and the young remain inshore until midsummer (Gordon 1968) by which time they would have been sharing this habitat with huge numbers of young alewives and many adults.

Deepwater sculpin

The deepwater sculpin declined markedly in abundance in Lake Michigan after 1960, on the basis of experimental sampling in the southeastern portion. (This species has not been used commercially except for small quantities taken in trawls in the early 1960's for the animal-food market.) Identical trawls fished off Grand Haven, Michigan, at the same depths on nearly the same dates took an average of more than four times as many deepwater sculpins in 1960 as in 1970. In standardized trawl series off Saugatuck, Michigan, in mid-April of each year 1964-71, the total numbers of deepwater sculpins caught in the successive years were 835, 409, 251, 179, 157, 76, 104, and 105. The somewhat larger numbers in 1970 and 1971 were due mostly to an influx of small individuals. No individual measurements were made, but the average weight (in grams) of deepwater sculpins in the catches climbed from 21 in 1960 to 24-25 in 1964-68, then dropped to 19 in 1969 and (off both Grand Haven and Saugatuck) 11 in 1970, and increased slightly to 12 in 1971. The increase in average size from 1960 to 1964-68 was due to a decreasing level of reproduction; few very small individuals were in the catches of 1964-68. The appreciably smaller average size in 1970-71 reflected a noticeable improvement in reproduction.

The decline in abundance of deepwater sculpins in the mid-1960's (and probably in the early 1960's) was a result of the above-described deficiency in recruitment. The alewife probably was responsible for the poor reproduction, because the decline in reproduction and subsequent improvement occurred during the buildup and decrease, respectively, of the alewife populations. Alewives in Lake Michigan are concentrated in deep water in winter when the deepwater sculpin spawns (as indicated by gonad condition at various times of the year-unpublished data, Great Lakes Fishery Laboratory). As mentioned previously, alewives are known to feed on fish eggs in Lake Michigan and might well include the eggs of deepwater sculpins in their diet. Alewives might also compete with larval sculpins for plankton food or prey upon them; although adult alewives are in shallow water when eggs of deepwater sculpins hatch in spring (unpublished data, Great Lakes Fishery Laboratory) many immature alewives probably remain in the deeper areas at that time. But even aside from this possibility, alewives had so decimated the populations of large species of zooplankton in Lake Michigan by the mid-1960's (Wells 1970) that the actual presence of alewives among deepwater sculpin fry may not have been necessary to exert an adverse effect on them.

The future of deepwater sculpins in Lake Michigan is uncertain. The increase in reproduction in the late 1960's, which was probably related to the decrease of alewives, may be reversed if the alewife's recent (1969-70) recovery continues. Deepwater sculpins are scarce or lacking in Lake Ontario, where they were once abundant (Wells 1969); Smith (1970) implied that the alewife was primarily responsible. Deepwater sculpins continue to be abundant in Lake Huron (unpublished data, Great Lakes Fishery Laboratory), in spite of the large numbers of alewives present (Smith 1970) (unfortunately, however, no data are available on their abundance before the invasion of the alewife). Perhaps this abundance is due to the more oligotrophic nature of Lake Huron (as compared with Lakes Ontario and Michigan), which may favor the deepwater sculpin and permit it to withstand better the influences of the alewife.

Spoonhead sculpin

The Spoonhead sculpin, which once was common lakewide in Lake Michigan (Deason 1939) has decreased progressively in numbers and is now rare or absent in the southern portion. Several specimens were observed in trawl catches made by the Great Lakes Fishery Laboratory in that area in 1954, but none in extensive trawling in 1960 and 1964-71. Although an occasional specimen might have been overlooked among slimy sculpins, it is doubtful that many would have gone undetected. The present status of the Spoonhead sculpin in northern Lake Michigan is not known; one was caught by trawl from the *Cisco* off Ludington in 1971. Wright (1968) observed several in 1966 in stomachs of Lake Michigan lake trout which were presumably taken from the northern part. No causes are suggested for the apparent disappearance of the Spoonhead sculpin in southern Lake Michigan.

Ninespine stickleback

Ninespine sticklebacks have increased in abundance in southern and east central Lake Michigan in the past few years, but data are lacking for the northern part of the lake, where the species is most common. Catches in standard trawl series off Saugatuck, Michigan, in mid-April 1964-71 were 0, 0, 1, 0, 0, 1, 13, and 60 in the successive years; in standard trawl series off Ludington in late October-early November 1967-70 the figures were 0, 41, 102, and 634. The increase might be related to the decrease in abundance of alewives but unfortunately no data for pre-alewife abundance of ninespine sticklebacks are available. Future surveillance of population changes of both species should establish whether or not such a relation exists.

Other species

Data for the other common fish species of Lake Michigan either are not adequate to evaluate trends in abundance, or do not indicate definite trends. Several of these species confined mostly to Green Bay have been of minor commercial importance. Production of northern pike averaged 46,000 pounds in 1899-1970 (highest 255,000 pounds in 1908). Catches of freshwater drum averaged 29,000 pounds in 1899-1962 (highest 139,000 pounds in 1944); the catch since 1962 has been negligible, due to poor market demand. Production of catfish (including channel catfish and bullheads) averaged 89,000 pounds in 1889-1970 (highest 387,000 pounds in 1945).

Several other species have not been taken commercially, but limited data on their abundance have come from experimental catches or other sources. Slimy sculpins were almost four times as abundant in 1970 as in 1960 in similar trawl tows (same depths, dates, gear) off Grand Haven. Identical trawl series off Saugatuck in mid-April of each year 196471 also showed a large population in 1970, but did not indicate a steady increase; total catches in the series during the successive years were 724, 490, 410, 825, 1,138, 582, 2,788, and 1,540. These changes may simply reflect normal fluctuations in abundance. Trout-perch and spottail shiners, on the basis of the mid-April sampling off Saugatuck, have shown no steady trends in abundance.

CONCLUSIONS

The far-reaching effects of man's activities on Lake Michigan's ecosystem have included changes in water chemistry, benthos, plankton, and native fish populations. Although the changes in water chemistry and lower biota have been generally modest (except locally), those in fish stocks have been vast. The changes in native fish stocks (mostly decreases in abundance) are primarily attributable to exploitation, the introduction of exotic fish species, and accelerated eutrophication and other forms of pollution.

Exploitation was easily the major factor causing changes in Lake Michigan's fish stocks until the smelt became abundant in the 1930's, and probably until the sea lamprey became well established in the 1940's and the alewife in the 1950's. The commercial fishery continued to influence native fish populations after the invasion of the exotics into Lake Michigan, but since their entry the impact of at least the sea lamprey and alewife has been much stronger than that of the fishery. Accelerated eutrophication and other pollution, although certainly important, have been less decisive than the other factors in bringing about changes in the native fish stocks of Lake Michigan.

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