LAKE HURON

The Ecology of the Fish Community and Man's Effects on It

Great Lakes Fishery Commission

TECHNICAL REPORT No. 21

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.

LAKE HURON
The Ecology of the Fish Community and Man's Effects on It

by

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TECHNICAL REPORT No. 21

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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. Numann of West Germany. After two years of preparation, a work party consisting of approximately 2.5 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
H. A. Regier

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by

A. H. Berst and G. R. Spangler

ABSTRACT

Lake Huron is a large, deep, oligotrophic lake, centrally located in the St. Lawrence Great Lakes system. Manitoulin Island and the Bruce Peninsula divide the lake into the relatively discrete water masses of the North Channel, Georgian Bay, and Lake Huron proper. Water quality in Lake Huron has deteriorated only slightly from the conditions which existed in the early 1800's. The only significant changes are confined to areas adjacent to centers of human activity, chiefly Saginaw Bay and various harbours and estuaries in Georgian Bay and the North Channel. The lake has supported a commercial fishery which has produced annual catches as high as 13,000 metric tons. A dramatic decline in landings of commercially valuable species and an instability in fisheries resources has occurred in all areas of the lake since the 1940's. This depression of the populations of valued species was associated with the accidental introduction of the sea lamprey, instances of overfishing, and deterioration of water quality in Saginaw Bay. The present depressed state of the fisheries will undoubtedly persist until sea lamprey control is achieved and climax predators are re-established. Governments are proceeding toward the establishment of water quality criteria and fishery management practices which, hopefully, will stabilize the fisheries and prevent further deterioration of the aquatic environment.

INTRODUCTION

Lake Huron, one of the four Great Lakes shared by Canada and the United States, occupies a central position in the St. Lawrence Great Lakes system. In addition to its strategic position in the St. Lawrence Seaway, the lake provides a recreational resource which attracts millions of people each year. It also supports a substantial commercial fishery, which has produced annual catches as high as 13,000 metric tons. During the past 4 decades, the fishery has been adversely affected by a number of factors which have resulted in drastic declines in landings of commercially valuable species.

The main objectives of this paper are to describe the dynamics of the fishery resources in Lake Huron, with emphasis on factors affecting the fisheries, especially changes in levels of exploitation, introductions of exotics, and changes in water quality.

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[1] Contribution No. 71-26 of the Research Branch of the Ontario Department of Lands and Forests, Maple, Ontario.

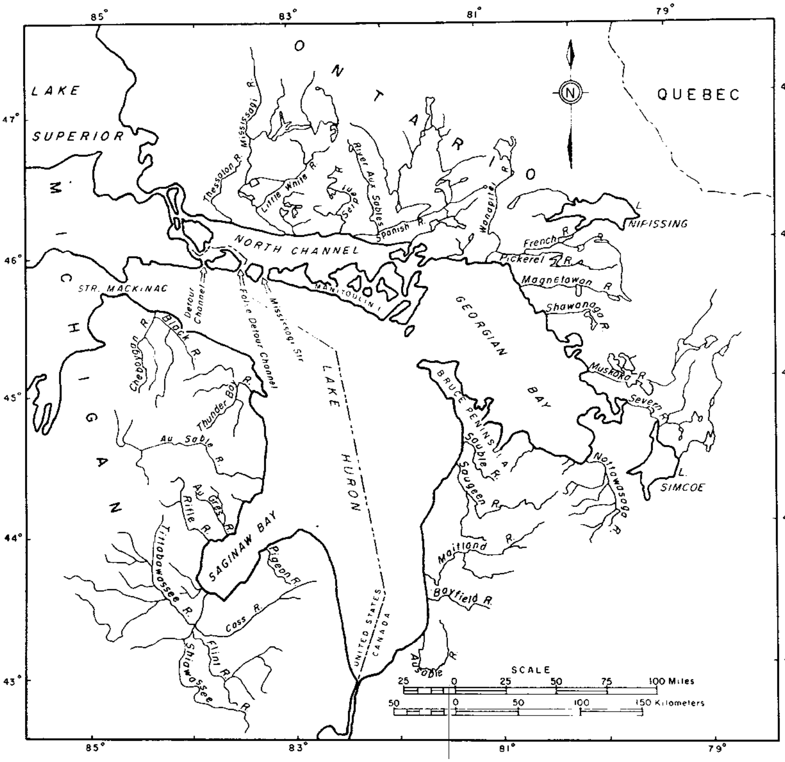

Figure 1. Lake Huron watershed, showing major tributaries.

PHYSIOGRAPHY AND

Lake Huron is the fifth largest lake in the world. It is 330 km long, 293 km wide, and occupies 32% of its 186,480 km^2 watershed (Fig. 1). The volume of the lake is 3482 km^3. Manitoulin Island and the Bruce Peninsula effectively divide Lake Huron into the relatively discrete water masses of the North Channel, Georgian Bay, and Lake Huron proper. The main body of the lake includes the shallow embayment of Saginaw Bay. Lake Huron lies at approximately the same elevation as Lake Michigan (176.7 m above sea level); it receives the natural outflow from Lake Michigan (approx. 15.56 m^3 /sec) via the Straits of Mackinac and from Lake Superior (approx. 2080 m^3 /sec) via the St. Mary's River.

The northern shore of Lake Huron along the North Channel and northeastern side of Georgian Bay is mainly on the southern rim of the Precambrian Shield. A Niagaran dolomite (Silurian) formation extends through a chain of islands (including Drummond, Cockburn and Manitoulin) and the Bruce Peninsula. The remainder of the Lake Huron basin is mainly within the Paleozoic rock formation (Hough 1958). The northern and northeastern parts of the watershed are forested with broadleaf and coniferous species; the

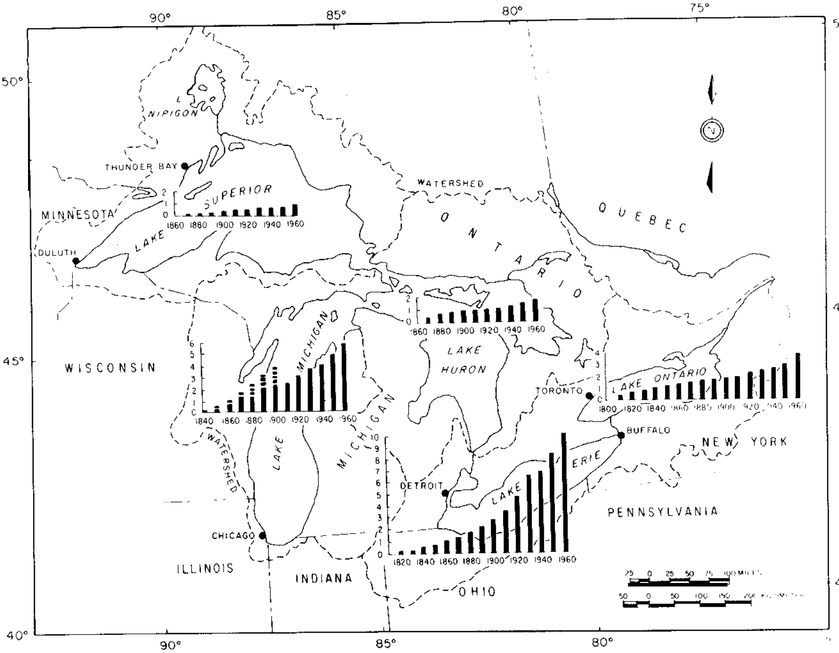

Figure 2. The St. Lawrence Great Lakes showing growth in human population. Bar. graphs show population in millions for every 10 years. (Re-drawn from Beeton 1969).

remainder is mainly farmland. Population growth has been relatively slow (Fig. 2) especially in the Canadian part of the basin, where the population increased only from about 414,000 in 1900 to 679,000 in 1960. On the U. S. side, the major urban centers, which are in the Saginaw River drainage area, accounted for an increase in population of almost 1 million during the same period.

The climate of the Lake Huron area fits the Continental Cool Summer category. The mean annual temperature is 5.8 C. Temperatures average 19.7 C in July, the warmest month, and 9.4 C in January, the coldest month (Thomas 1953). Lake Huron acts as a heat source for the surrounding region for more than half the year, and as a heat sink during a minor portion of the year (Ayers 1962). The area receives an average of 873 mm of precipitation annually. Prevailing winds are southwest in summer and southeast in winter.

The bathymetry of Lake Huron is shown in Fig. 3, and the area-depth profile of the 3 basins in Fig. 4. A prominent subsurface ridge extending across the lake from Alpena, Michigan, to Kincardine, Ontario, further divides the main basin into a long, deep trough (maximum depth 229 m) northeast of the ridge and a fairly regular basin (maximum depth 91 m) southwest of the ridge. This portion of the main basin includes Saginaw Bay. The outer half of Saginaw Bay is similar to the lake proper, but the inner part is shallow.

The North Channel is a shallow, well-enclosed passage with prominent bays and headlands imposed by the northern Manitoulin shore. North Channel

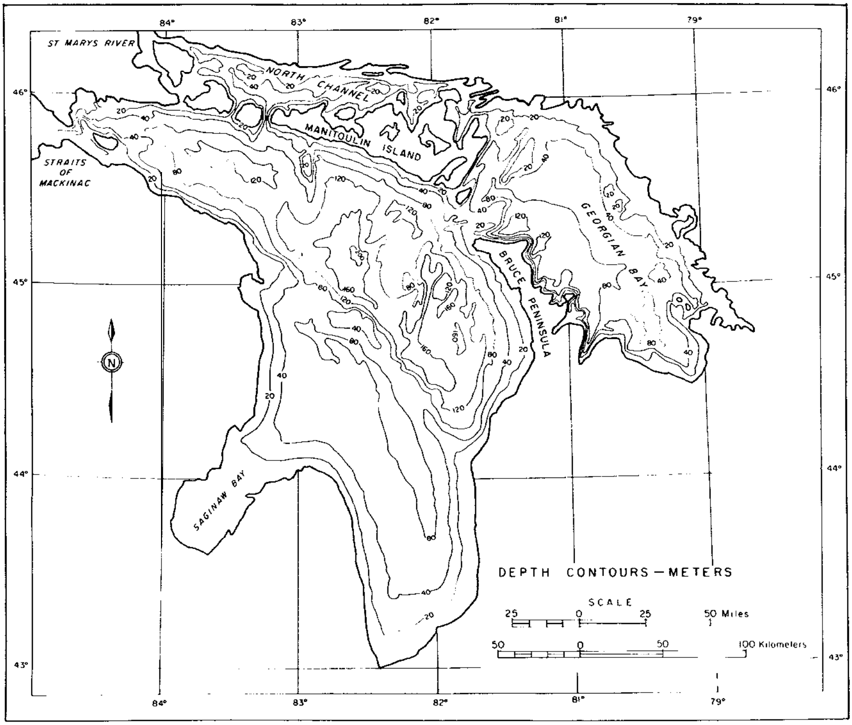

Figure 3. Bathymetric chart of Lake Huron. Contours interpolated from U. S. Lake Survey Chart No. 0.

waters enter the main basin at Mississagi Straits, Detour, and False Detour Channels at the west, and flow east into Georgian Bay through a narrow channel at Little Current, Ontario.

Georgian Bay is a relatively deep basin (30-1 10 m) with a highly irregular shoreline which includes over 20,000 islands. Georgian Bay is contiguous with Lake Huron proper through Owen, Fitzwilliam, and Lucas channels.

LIMNOLOGY

The morphometric differences between the North Channel, Georgian Bay, and Lake Huron proper impose a variety of restrictions upon limnological conditions in these areas. Beeton (1969) further recognized Saginaw Bay as distinctly different from the other three areas. Because limnological surveys of Lake Huron have necessarily concentrated upon one area at a time, a detailed discussion of lake-wide limnological features is not possible.

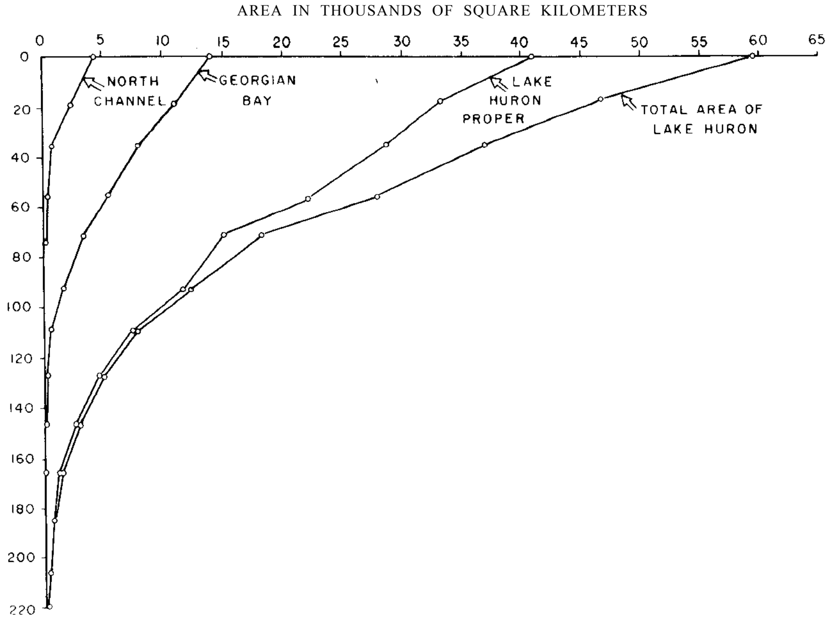

Figure 4. Area-depth profile of the main basins of Lake Huron. (From Anderson and Fry 1967).

Temperature

Anderson and Fry (1967) described the thermal characteristics of Georgian Bay from synoptic surveys conducted during the summers of 1953 and 1954. The 1953 survey set an example for the comprehensive synoptic surveys of the main basin carried out in 1954 (Ayers et al. 1956). McCombie (1967) presented a comprehensive description of the thermal regime of South Bay, an inlet of Lake Huron at the southeastern end of Manitoulin Island. Additional meteorological data have recently been collected from all three basins of Lake Huron by the Great Lakes Institute (Rodgers 1963, 1965; Anonymous 1964b).

The mean surface temperatures observed in the main basin of Lake Huron from spring to mid-summer are highest in shallow water and lowest over deep water. A thermocline is formed in late June in the southern half of the basin at 15-30 m and a well defined thermocline persists throughout August in depths of 15-38 m. In Georgian Bay the thermocline forms during July at 15-30 m. Bottom water temperature is 4.5 C or less throughout the summer below 45-60 m in the main basin and in Georgian Bay, but rises to at least 6.5 C in the North Channel.

Beeton et al. (1967) found that Saginaw Bay waters warmed rapidly in the inner bay during June and became homothermous by late July. The outer half of the bay warmed rapidly during June but the deeper waters were apparently influenced to a considerable extent by Lake Huron water from the main basin.

South Bay waters begin to warm in April and become stratified in June. Mean monthly surface water temperatures in the bay have been shown to be closely correlated with the mean monthly air temperatures during the open-water season (McCombie 1959). Average surface water temperatures reach a maximum of about 19 C in August and a minimum of about 1 C in late March. South Bay becomes vertically isothermal at about 7 C in November (McCombie 1967).

Lake Huron proper normally remains open throughout the winter, but shore ice covers the bays and may extend as far as 16 km into the lake (Beeton and Chandler 1963). Georgian Bay is generally covered with pack ice which shifts about under the influence of the wind. The North Channel freezes over in January and forms a relatively strong ice bridge between Manitoulin Island and the mainland until the breakup, which generally occurs during the last half of April.

Transparency and circulation patterns

Ayers et al. (1956) found that it was possible to trace Lake Michigan water in the Straits of Mackinac by its characteristically high transparency (11-16 m) during June and July. Lake Superior water in Mississagi Strait, Detour Channel, and False Detour Channel yielded transparencies of 3-9 m (white Secchi disc readings). Saginaw Bay transparencies ranged from 4-12 m in the outer bay to less than 3 m in the inner bay during June and July. Transparencies in the main basin were generally low (2-8 m) near shore and higher (12-14 m) in mid-lake during most of the summer.

From transparency measurements of Saginaw Bay, Beeton (1958) determined that circulation in the bay was usually counterclockwise. Beeton et al. (1967) further noted that northeast, east, or southeast winds produced a clockwise circulation and west or southwest winds a counterclockwise circulation.

Surface currents running southeast from the Straits of Mackinac to Alpena, Michigan, are evident during the summer (Ayers et al. 1956). Counterclockwise eddies are present in the surface circulation northeast of the Alpena-Kincardine ridge (Fig. 3). Surface currents travelling shoreward are probably responsible for the areas of sinking surface waters along the eastern shore of the main basin. Upwelling is commonly observed along the south Manitoulin shore and along the lower Michigan shore. In the presence of a well defined thermocline, upwelling waters are drawn mainly from the thermocline (Ayers et al. 1956).

Fry (1956) described an easterly drift of surface water across Georgian Bay in response to prevailing summer winds. Areas of sinking water occurred in the northeast corner of the bay and along the eastern shore, while areas of persistent upwelling were along the east end of Manitoulin Island and the eastern shore of the Bruce Peninsula. Fry (1956) found no evidence of a major exchange of Georgian Bay surface water with that of the main basin of Lake Huron.

Thermal bar formation occurs during the spring and fall on the Great Lakes (Rodgers 1965). It is defined as the region of vertical mixing between two water masses, one of which is warmer than 4 C, while the other is cooler than 4 C. The thermal bar can effectively control the horizontal movement of surface waters, impounding runoff and warmer water near shore in the spring. The thermal bar has been described for the main basin of Lake Huron near Douglas Point (Rodgers 1965) and probably also occurs in other areas of the lake.

Tides and seiches

True lunar and solar tides occur on the Great Lakes, but their amplitude is small (less than 5 cm) and they were considered to be of little importance relative to vertical movement induced by seiches (Horton and Grunsky 1927). Seiches with amplitudes in excess of 1 m have been recorded for Lake Huron (Ayers 1962); however, Bryson and Stearns (1959) found that a seiche amplitude of only 2 cm might result in a mixing as great as 10% per day of Lake Huron water with that of the outer basin of South Bay. The general effects of seiches on aquatic communities in the Great Lakes have not been described, but Emery (1970) attributed mortalities of crayfish (Orconectes propinquus) and sculpins (Cottus *bairdi)* to a rapid change in bottom water temperatures resulting from a seiche in Georgian Bay.

Chemical characteristics

The major sources of water for Lake Huron are the discharges from Lakes Superior and Michigan. Ayers et al. (1956) reported a conductivity of 140-145 micromhos/cm for Lake Huron in the region of mixing of the parent water masses. This is nearly identical with a value of 143 micromhos/cm calculated for a mixture of Lake Michigan and Lake Superior waters (Kramer 1964). The influence of the Lake Huron watershed is made apparent by the increase in conductivity to values of 170-175 micromhos/cm at the outlet of the lake (Ayers et al. 1956). Conductivities in the main basin closely parallel the distributions of calcium and magnesium. Conductivities range from 110-166 micromhos/cm in the North Channel and from 123-167 micromhas/cm in Georgian Bay (Anonymous 1964b). Total dissolved solids reported for Lake Huron in recent years range from 110-134 ppm (Ryder 1965; Beeton 1965, 1969; Ayers 1962). Dissolved oxygen concentrations are at saturation levels throughout the year at all depths except in Saginaw Bay where Beeton et al. (1967) found a value as low as 66% at a depth of 9 m after a period of calm weather.

Biological aspects

No long-term studies of Lake Huron phytoplankton or zooplankton have been published, but Williams (1962) reported that diatoms dominated the phytoplankton collected at the outlet of Lake Huron during the period May 1960 to June 1961. Seasonal peaks in abundance occurred during November, January, and April. The most abundant diatoms were *Fragilaria, Tabellaria,* and *Cyclotella. Karatella* and *Polyarthra* were the most abundant rotifers.

Only qualitative studies of plankton in Georgian Bay have been published. Bailey (1925) and MacClement (1915) listed the diatoms and presented a partial list of phytoplankton. Sars (1915) listed some cladocerans, copepods, and an ostracod taken in surface nettings.

Teter (1960) found that *Pontoporeia affinis* was the most numerous component of the bottom fauna of the main basin of Lake Huron, contributing 53% of the organisms from shallow water and 81% of those from deep water. Sphaeriid clams (Pisidium) made up 10% of the shallow water sample and 8% of the deep water forms. Oligochaetes, mainly *Limnodrilus claparedianus* and *Naidium* sp., made up 6% of the organisms from shallow water and 9% of those from deep water. Larvae and pupae of midges *(Tendipedidae)* were abundant in shallow water (16%), and the larvae were present in small numbers in deep water.

The relative abundance of *Pontoporeia,* oligochaetes, sphaeriid clams, and tendipedids reported by Schuytema and Powers (1966), for offshore waters of Lake Huron, agreed generally with the findings of Teter (1960). The density of benthic organisms was far greater in inshore waters and Saginaw Bay than in offshore waters. Amphipods were relatively more abundant in the main basin than elsewhere in Lake Huron and oligochaetes were abundant only in localized areas of the North Channel. Brinkhurst et al. (1968) found very few oligochaetes in samples from Georgian Bay, and among these the Tubificidae were relatively scarce. The presence of sphaeriid clams, especially *Pisidium conventus,* and the tendipedid *Heterotrissocladius* further characterize Georgian Bay as an oligotrophic body.

Cooper (MS 1964) found considerable numbers of oligochaetes, chironomids and sphaeriids at all depths sampled in South Bay. *Pontoporeia* was the dominant benthic organism at depths greater than 10 m. Among the oligochaetes, *Stylaria* was common at 10 m while *Tubifex* was most abundant at greater depths.

The benthos of Saginaw Bay was dominated by oligochaetes, which made up 78% of the population (Schuytema and Powers 1966). Major concentrations of oligochaetes (up to 49,000/m^2) were found near the mouth of the Saginaw River. Brinkhurst (1967) felt that the presence of *Paranais litoralis* in the inner bay was due to the brackish outflow of the Saginaw River. *Pontoporeia affinis* was the dominant amphipod near the mouth of the bay while *Gammarus* predominated in samples from the southern portion of the bay.

Productivity indices

Rawson (1952) considered morphometric, edaphic, and climatic factors as the major determinants of lake productivity. Using long term commercial fish production as an index, he demonstrated the importance of depth in the productivity of 12 north temperate lakes. His logarithmic regression of depth on productivity predicted a production of 1.4 kg/ha for Lake Huron; the reported actual production was 1.6 kg/ha. The mean depth of Lake Huron (59 m) definitely places it in the oligotrophic category.

Ryder (1965) defined a morphoedaphic index as the ratio of total dissolved solids to mean depth, and applied it to fish production for 23 moderately to intensively fished north temperate lakes. If this index is calculated separately for the three basins of Lake Huron, it is apparent that the main basin is the most oligotrophic body followed by Georgian Bay and the North Channel (Table 1). The production figures for the 192340 period

Table 1. Morphoedaphic index and theoretical and actual production of fish from Lake Huron.[1]

				Production (kg/ha)/yr		
					Actual	
Basin	Area[2] (km^2)	Mean depth (m)	Morphoedaphic index	Theoretical	192340	1941-60
North Channel	4,550	22	1.52	2.77	1.27	0.40
Georgian Bay	13,752	51	0.66	1.82	1.04	0.71
Main basin	41,659	61	0.55	1.66	1.70	0.85
Entire lake	59,961	55	0.61	1.75	1.52	0.75

[1] Morphoedaphic index calculated by assuming a value for total dissolved solids of 110 ppm for all areas of the lake. Theoretical production calculated by rapid approximation method (Ryder 1965). Actual production figures derived from Baldwin and Saalfeld (1962).

[2] Area and depth are approximate (planimetered from U. S. Lake Survey Chart No. 0); area includes islands smaller than 5 km^2.

are comparable to the theoretical values, whereas the data for 1941-60 show a dramatic decrease in the production of high value species.

Eutrophication

The natural aging process of Lake Huron is too slow to be of immediate economic interest but the extent to which human activity has accelerated this process or has contributed directly to eutrophication is a matter of prime concern to all users of the Great Lakes.

Ayers (1962) noted that the chemical history of the Great Lakes has been poorly documented. Earlier analyses frequently lacked an explanation of methodology, or were otherwise not comparable with those made in recent years. Clarke (1924) presented data on the chemical composition of Great Lakes waters based upon multiple samples taken from lake outlets throughout the year. Comparison of these values (Table 2) with those of Allen (1964) provides some idea of the absolute increase of certain ions in Lake Huron over the last 60 years.

Beeton (1965) noted that the major source of chlorides within the Lake Huron watershed was the Saginaw Valley, and attributed most of the increase

Table 2. Comparison of concentrations (ppm) of selected ions in Lake Huron from samples taken in 1906-07 and 1956. Data are from Clarke (1924) and Allen (1964).

	Year	
Ion	1906-07	1956
Calcium	24.0	26.7
Sodium + potassium	4.4	3.4
Sulphate	6.2	13
Chloride	2.6	5.9

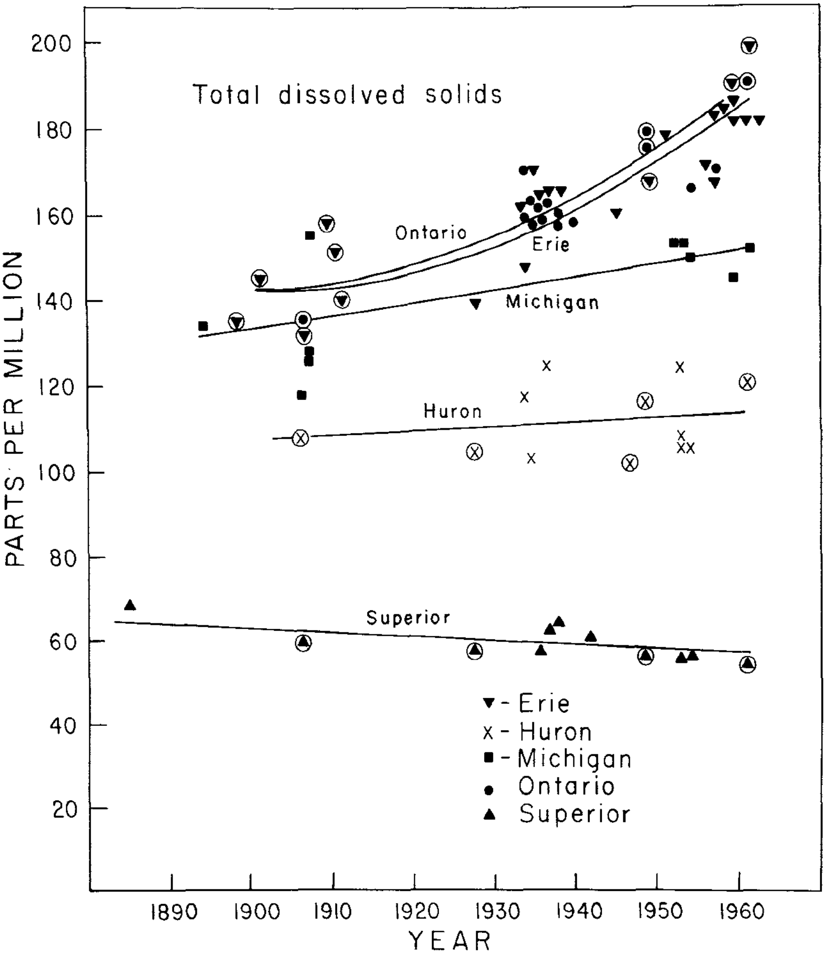

Figure 5. Concentrations of total dissolved solids in the Great Lakes. Circled points are averages of 12 or more determinations. (From Beeton 1965).

in the lake water values to the production of brine in the oil fields and for chemical industries. Sulphate concentrations had increased 7.5 ppm over the past 54 years.

The slight increase in total dissolved solids in Lake Huron in 1907-60 (Fig. 5) is probably real since about 30% of the inflow to Lake Huron is from Lake Michigan (Beeton 1965). Total dissolved solids did not change significantly in Lake Superior during this interval but increased about 20 ppm in Lake Michigan. Beeton (1969), who calculated magnesium, calcium, and sodium concentrations for Lake Huron based upon the content and rate of inflow of Lake Michigan and Lake Superior water, found that observed concentrations of these ions were within 1 ppm of the calculated values. Chloride, sulphate, and total dissolved solids were 2 to 10 ppm greater than calculated values, suggesting an additional nutrient source within the Lake Huron basin.

Increases in total dissolved solids and in the concentrations of certain ions have probably not occurred at a uniform rate throughout the last 60 years. Kramer (1964) estimated that a minimum of about 22 years would be required to effect a marked increase or decrease of a nutrient throughout the entire lake. Winchester (1969) called this the “residence time” (his estimate was 20 years for Lake Huron) and defined it as the average time dissolved materials and water spend in a lake before transport through the normal outflow channel. Considering this time element, it is entirely likely that the present rate of eutrophication is accelerating much more rapidly than the data in Table 1 and Fig. 5 suggest at first glance.

Changes in species composition or relative abundance indices can often serve as indicators of eutrophication. The presence of large concentrations of the relatively pollution tolerant oligochaete *Limnodrilus hoffmeisterii* was taken by Brinkhurst (1967) to be an indicator of the influence of the heavily polluted Saginaw River in Saginaw Bay. A combination of these large concentrations with a low abundance of “clean-water” associates such as the mayfly *Hexagenia limbata.* distinguishes areas of gross organic pollution in Saginaw Bay. The filamentous green algae of the genus *Cladophora* have been used as indicators of pollution in the lower Great Lakes (Neil and Owen 1964) but apparently Lakes Huron and Superior lack the basic fertility for even marginal growths of *Cladophora.* Concentrations of *Cladophora* identified in Lake Huron proper and Georgian Bay were found associated with sewer outfalls and this genus was considered by Beeton (1966) as an indicator of local pollution.

Forest products industries have had a significant effect upon the ecology of Lake Huron. Sawdust pollution was known to have adversely affected the spawning of lake whitefish *(Coregonus clupeaformis)* in the Saginaw Bay area as early as 1845 (Beeton 1969). Large rafts of logs traversed Georgian Bay during the period 1885-1900 and bark from these rafts undoubtedly littered a considerable portion of the lake bottom (Barry 1968). Rafting of logs has only recently been discontinued on the open waters of the lake, but logs are still driven on tributary streams, and bark litter is known to be a problem to the operation of commercial fishing gear in the North Channel. The discharge of wood fibers from pulp mills has also polluted some tributary streams. Chemical contaminants from pulp mills are known to adversely affect the quality of fish products (Ryder 1968).

Reports of the accumulation of chlorinated hydrocarbons and mercury compounds in the Great Lakes system have been widely publicized. Although there are no documented cases of mass die-offs of fish in the Great Lakes related to these pollutants, the tissues of various species are known to contain appreciable concentrations. Average DDT levels in muscle tissues of representative fish species in the Great Lakes range from 0.40 for Lake Erie to 4.44 ppm for Lake Michigan and are 2.35 ppm for Lake Huron. Preliminary tests of mercury levels in tissue samples of representative fish species from southern Lake Huron, Georgian Bay, and the North Channel show mean value of 0.44, 0.25, and 0.22 ppm, respectively. The higher value for the Lake Huron sample probably reflects the mercury levels in walleyes *(Stizostedion vitreum)* and white bass *(Morone* chrysops) which migrated into Lake Huron from Lake St. Clair, where mercury pollution is known to be relatively severe.

Waste heat production from electric generating stations is a potential environmental problem. The effects of thermal pollution will not be known on a lakewide basis for some time, but it seems likely that an increase in biological production may characterize areas affected by thermal outfall plumes. Radioactive contamination of the lakes remains a distinct possibility, both from nuclear powered generating plants and, more directly, from the mining of radioactive ores within the Lake Huron basin.

ECOLOGY

Lake trout

Habitat

Lake trout *(Salvelinus namaycush)* in North America normally inhabit cool, oligotrophic lakes. Their depth distribution varies from lake to lake, and within each lake according to seasons. They are widely dispersed in shallow waters in spring, and occupy deeper strata in summer, where the temperature ranges between 4.4 and 18.3 C (MacKay 1963). The preferred temperature of lake trout under laboratory conditions is 11.7 C (McCauley and Tait 1970). Ferguson's (1958) summary of published data on lake trout distribution in inland lakes, including waters in Maine, New York, and Ontario, indicated that the trout were found at temperatures from 8 to 15.5 C.

In the Great Lakes, most lake trout live in waters shallower than 110 m, although they penetrate the greatest depths that have been fished with nets (229 m). In southern Lake Huron, lake trout were usually found in water deeper than 30 m. Trout in the area north of Saginaw Bay were scarce in summer in less than 30 m of water and the inshore population appeared to shift to progressively deeper water as the season advanced from July to October. In the Alpena region the trout moved from depths greater than 30 m in May to a 12-21 m range in June, then returned to progressively deeper areas until September (Van Oosten 1944).

In Georgian Bay, lake trout were captured in almost every fishing area, with the exception of the very shallow south-east section of the bay. They were taken in relatively deep water (36-55 m), generally close to islands or reefs, during the summer and on the many shoals and reefs in the autumn. The deep-water lake trout or "siscowet" was also reported to have inhabited the depths of Georgian Bay (Anonymous 1893).

Few small trout were seen in the commercial catches. Tomkins (MS 1951) found that lake trout less than 38 cm long were captured mainly in nets set for deep-water chubs *(Coregonus* spp.) in water 80 to 110 m in depth. Martin (1956) reported that in two Algonquin Park lakes, smaller and younger lake trout were generally found at greater depths than larger and older fish.

Food and feeding habits

Young lake trout fed upon a variety of invertebrates and small fish in Georgian Bay (Tomkins MS 1951) and in Lake Michigan (Van Oosten and Deason 1937). There is no evidence that cannibalism occurred to any extent in the lake trout population in Georgian Bay. Tomkins (MS 1951) found no lake trout among the 7 species of fish identified from the stomach contents of 619 lake trout of various ages caught at a variety of depths in Georgian Bay. Since cannibalism by lake trout occurs under hatchery conditions, Tomkins' evidence lends support to the belief that the distribution of small lake trout differs from that of large ones.

Age and growth

The lake trout is one of the largest freshwater fishes of North America. Specimens in excess of 45 kg have been reported from various inland waters; the largest authenticated record is a 46 kg fish captured in 1961 in Lake Athabaska (Scott 1967). The average weight in the commercial catches from the Great Lakes varied with locality, season, and gear from 1.5 to 5 kg. Few fish heavier than 11 kg were captured by the commercial fishery (Van Oosten 1944). Hamilton (1893) recorded that the combined weight of two Georgian Bay lake trout was 110 pounds (50 kg) "with not a pound of difference between the two fish."

Growth curves of native lake trout from Georgian Bay, planted lake trout from South Bay, and F_1 splake *(Salvelinus fontinalis X S. namaycush)* from Lake Huron show that native and planted trout grew slower than the hybrids (Fig. 6). By age IV the mean length of the Lake Huron hybrids was 53.6 cm, while Georgian Bay trout averaged 36.9 cm and South Bay trout *48.3* cm.

Reproduction

Tomkins (MS 1951), who examined the gonads of 697 lake trout of ages II to X from Georgian Bay, found that males younger than age V and females younger than age VI were immature; all males were mature at age VIII and females at age IX. This is comparable to the maturation of lake trout in South Bay (Budd and Fry 1960) and Lac la Ronge (Rawson 1961).

Lake trout throughout their range may spawn as early as June (Eschmeyer 1955) and as late as December (Martin 1956). In the North Channel lake trout spawned about 1 week before those in Lake Huron proper, where spawning took place from October 20 to November 10 (Smith, J. B. 1968).

Lake trout spawning occurs at a temperature of approximately 9-12 C (Martin 1956; Rawson 1961; De Roche 1969). No information is available on the incubation period of lake trout eggs in Lake Huron. De Roche (1969) collected eggs and sac fry during March from Thompson Lake, Maine, when water temperature on the spawning beds was approximately 1.1 C. Martin (1956) found that the time of hatching in Algonquin Park lakes in Ontario extended from mid-February to late March, an incubation period of 15 to 21 weeks. The fry had left the spawning beds before mid-May.

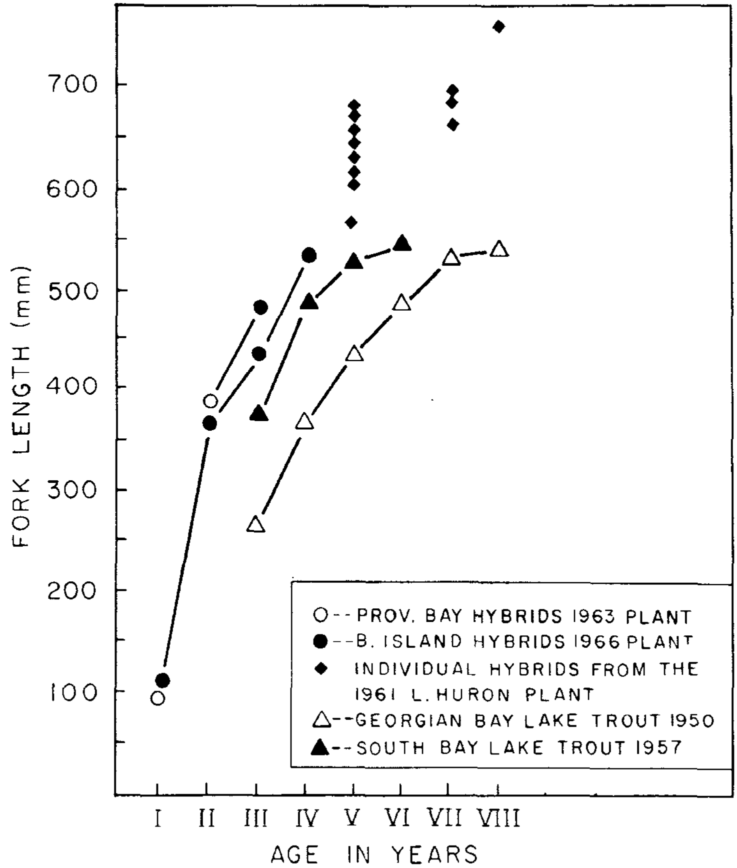

Figure 6. Growth of native lake trout in Georgian Bay (Tomkins MS 1951), planted lake trout in South Bay (Budd and Fry 1960) and F_1 splake in Lake Huron (Berst and Spangler 1970). The plotted points for the Providence Bay and Burnt Island Bay plantings are averages for fish taken in June of each year from gill nets and pound nets, respectively. Budd and Fry's data were from June pound net catches, and Tomkins' from June samples taken by large mesh gill nets and baited hook lines. Lengths of individual splake from the 1961 planting show the growth trend of fish older than age IV.

Natural mortality

Lake trout frequently live to an age of 15 years or more in lightly exploited populations. Loftus (1958) reported lake trout up to 14 years of age in two river-spawning populations in eastern Lake Superior. Rawson (1961) showed 8.9% of 160 lake trout taken from Lac la Ronge in 1958 to be 13 to 16 years of age. The oldest lake trout mentioned by Tomkins (MS 1951), who summarized age data for lake trout from various waters including the Great Lakes, was an l&year-old fish of 20 kg from Georgian Bay.

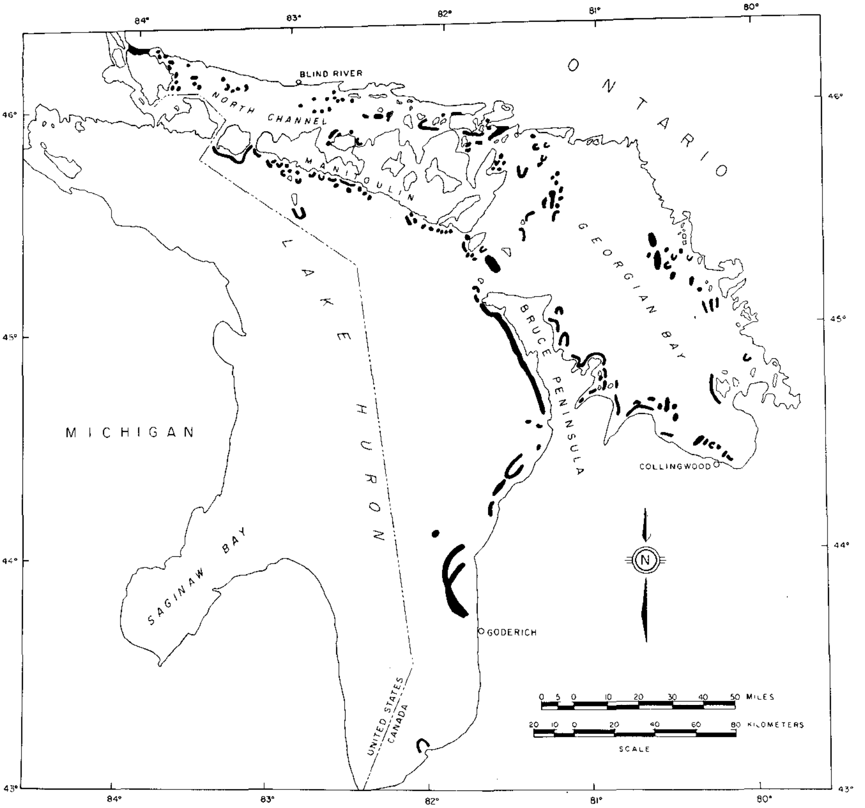

Figure 7. Former lake trout spawning grounds in the Canadian waters of Lake Huron. Solid black areas indicate approximate location and extent of spawning areas. (From Smith, J. B. 1968).

An unusually high natural mortality of lake trout in South Bay of Lake Huron was described by Fry (1953): the 1944 year class of native fish, which first entered the fishery in 1947, was virtually extinct by 1952. During this interval the natural mortality rate suddenly increased from a value of 25% per year to 60-70% when the trout had attained a size at which they were vulnerable to attack by the sea lamprey, *Petromyzon marinus*. Fry (1953) concluded that the major cause of natural mortality suffered by this year class between 1947 and 1952 was lamprey attack. The mortality rate was so severe that no substantial lake trout spawning occurred in South Bay after 1944 or 1945.

In South Bay the natural mortality of 10,100 yearling lake trout planted in 1951 and 23,100 planted in 1952 was so high that only 2% of each planting was estimated to have survived to age V (Fry 1958). Budd and Fry (1960) concluded that, although survival of the planted fish was good to age IV, the stocks were completely eliminated by the lamprey before any of the females reached maturity at age VII.

All available evidence indicates that the lake trout is extremely vulnerable to lamprey attack. Even if lamprey abundance can be held at a low level, we believe that the lake trout's susceptibility to attack by the residual lamprey population renders the prospect for economically sound trout management doubtful.

Coregonines

Systematic status

Koelz (1929), who made the first, and still the most comprehensive, treatment of this group of fishes in North America, distinguished 11 species and 7 possible subspecies of the family Coregonidae in the Great Lakes. The Lake Huron forms included the lake whitefish, round whitefish, *Prosopium cylindraceum,* shallow-water cisco, *Coregonus artedii,* and the following chub species: *Coregonus johannae, C. alpenae, C. zenithicus, C. nigripinnis, C. kiyi,* and C. *hoyi.*

Koelz believed that the Great Lakes coregonids were differentiated before the Great Lakes attained their present form, and that many racial distinctions originated during the 20,000 years that geologists estimate have elapsed since the formation of the present Great Lakes.

Bensley (1915) noted that fishermen of southern Georgian Bay recognized two types of *C. clupeaformis* and felt that there was some evidence on which to base a distinction between the coarse-scaled or shoal whitefish and the more typical deep-water form. His preference, however, was not to recognize the local variant as a distinct race. More recently, Lindsey et al. (1970) have reviewed the taxonomic status of this species and have considered all deep-bodied Great Lakes forms as belonging to *a "Coregonus clupeaformis* species complex", thus obliterating sub-specific designations in the Great Lakes forms.

The genus *Leucichthys* is included by some authors in the genus *Coregonus* but recent electrophoretic and immunological studies of serum proteins (Chellevold 1970) show a clear distinction between these groups. We have adopted the convention of Coreganinae for the whitefish sub-family in the family Salmonidae and accept Behnke's (1972) recognition of *Leucichthys* at the sub-generic level.

Habitat

The species and their varieties in the sub-family Coreganinae inhabit the cool waters of the Great Lakes and the deeper inland lakes. *Coregonus clupeaformis, C. artedii,* and *Prosopium cylindraceum* are shoal-loving forms; *C alpenae, C. zenithicus,* and C. *hoyi* also inhabit comparatively shallow water; *C. johannae, C. nigripinnis* and *C. kiyi* are the deep water forms and are usually found at depths of 55 to 180 m. The bathymetric distribution of the species or groups of species is zonal. Each occupies a rather broad zone defined by the depth of water at its margins. At the center of the zone each has its greatest density of population (Koelz 1929).

Reighard (1910) described the areas of Lake Huron where whitefish were ordinarily taken by commercial fishing gear. This habitat consisted of a zone 1 to 33 km wide along the entire shore where the depth of water ranged from 18 to 64 m. In Lake Huron proper, this zone encloses a central area of deep water, which Reighard believed to be an effective physical barrier, separating the whitefish populations on either side of the lake. Whitefish were apparently found in all areas of the North Channel. In Georgian Bay the greater part of the area is composed of whitefish grounds. Here, displacement of the deep water toward the southwest leaves the marginal whitefish area very narrow on the southwest side of the bay and very broad on the northeast side. Cucin and Regier (1966) felt that whitefish have inhabited the 0 to 46 m depth zone in Georgian Bay in recent years. Whitefish are found throughout the entire North Channel.

Little is known about the responses of the various species of coregonines to physical and chemical factors of their environment. Although Ferguson (1958) reported a preferred temperature of 12.7 C for 2-year-old whitefish and Reckahn (1970) reported that young-of-the-year whitefish are associated with the 17 C isotherm in mid-summer in South Bay of Lake Huron, thermal distribution data for other coregonines in the Great Lakes have not been published.

Koelz (1929) believed that differences in the character of the bottom indirectly influence the distribution of the various species. He pointed out that all species with the exception of *C. artedii,* a plankton feeder, are confined to a bottom stratum of water no more than 1.5 m thick. In this stratum they find their food, which consists chiefly of various species of Crustacea and Mollusca.

The seasonal movements of whitefish in Lake Huron were described by Van Oosten (1939). Whitefish are gregarious and travel in schools. In spring and early summer they concentrate in water less than 18 m deep; in July and August they migrate into deeper water. In Lake Huron, their maximum density in summer is between depths of 24 and 34 m. They return in the fall to shallower water, where they probably remain until the ice breaks up. Budd (1.957) concluded that recapture patterns of 4383 whitefish tagged in South Bay of Lake Huron indicated a major migration into Georgian Bay in early summer. The fish remained in Georgian Bay through the winter, and returned to South Bay the following spring. Of 1518 whitefish tagged and released in Lake Huron and Georgian Bay, none were recovered in South Bay. Discrete populations of whitefish have since been reported for Georgian Bay (Cucin and Regier 1966), South Bay (Budd et al. MS 1963), Lake Huron proper (Spangler 1970), and for areas in Lakes Michigan and Superior.

Reproduction

Most of the species of coregonines in Lake Huron are separated by spawning seasons and grounds. The three shoal forms *(clupeaformis, cylindraceum,* and *artedii)* spawn in November and early December, but it is not known that they congregate on the same grounds at the same time. The earliest spawner, *nigripinnis,* spawns in January at depths of about 110 m; *johannae* spawns in August or September, presumably at depths of 110 m;

zenithicus spawns in late September and early October; and *kiyi* in early November (Koelz 1929).

Whitefish in Lake Huron spawn on sand, gravel, stone, or honeycomb rock at depths of 2 to 18 m during November and the first half of December (Van Oosten 1939). Van Oosten found that 8894% of the males of age groups III to V and all older males were sexually mature or maturing. Females matured later in life: none were mature at age III, about 34% were mature at age IV, and all were mature by age VII. The ratio of males to females was approximately 1: 1. Cucin and Regier (1966) found that whitefish reproduction in Georgian Bay depended largely on males age IV and older and longer than 43 cm and females age V and older and longer than 46 cm.

The incubation period of clupeaformis in Lake Huron spans the interval of mid-November to the following April. It has been suggested that temperature changes during this incubation period may considerably influence the strength of whitefish year-classes by affecting hatching times and the development of fertilized eggs. Price (1940) incubated whitefish eggs at constant temperatures over the range 0-12 C and found that the optimum temperature was 0.5 C. Colby and Brooke (1970) found that the optimum temperature range for normal development of *artedii eggs* was 2-8 C.

Upon hatching in mid-April, whitefish fry rise to the surface over the spawning grounds, remain for a few days, and then make their way or are carried by the currents inshore, where they tend to concentrate in water less than 1 m deep. Feeding begins when the yolk sac is absorbed. By the end of May, whitefish are rare in shallow water (Hart 1930; Faber 1970). During July and August, young-of-the-year whitefish in South Bay may be found in the upper levels of the metalimnion. With the approach of autumn the young fish apparently descend into the hypolimnion (Reckahn 1970).

Growth and mortality

Growth rates of whitefish vary widely throughout the Great Lakes. Data for Georgian Bay also show a considerable variation in growth between and within year classes. The 1943 year class, which was by far the largest year class ever recorded for Georgian Bay, grew very slowly, requiring almost 15 years to attain a weight of 2 kg. This is in contrast with the year classes of 1951 to 1957, which attained this weight in 7 to 8 years (Cucin and Regier 1966).

The longevity of a year class of whitefish depends partly on the size of the year class and the intensity of the exploitation to which it is subjected. Van Oosten (1939) found all age groups from III to XII present in commercial catches from Lake Huron proper in 1923 and 1924. Cucin and Regier (1966) showed the remarkable persistence of the 1943 year class of whitefish in southern Georgian Bay. Even in the presence of a relatively intensive fishery, whitefish from this year class were present in substantial numbers at ages XIV to XIX.

Unexploited populations of whitefish have not been described for Lake Huron, but Edsall (1960) found age groups II to XII present in an unexploited population in Munising Bay of Lake Superior. These fish grew very slowly and matured at ages VI to X. Kennedy (1953) reported whitefish older than 20 years, including one specimen of age XXVIII, in samples from the commercial fishery of Great Slave Lake in Canada's Northwest Territories.

Total annual mortality rates of 61, 57, 74, and 81% were reported by Kennedy (1953, 1963) for Great Slave Lake and for three unexploited lakes in northern Canada. Roelofs (1958) found a total annual mortality rate of 94% for age III whitefish in Lake Michigan but was unable to segregate fishing mortality from that due to other causes. Cucin and Regier (1966) estimated total annual mortality rates of 77 to 80% for 5-and B-year-old whitefish in Georgian Bay and showed that 79 to 85% of these fish had been taken by the fishery. They felt that a mortality rate of 34% per year in the absence of a fishery was realistic for Georgian Bay. Spangler (1970), who described the seasonal pattern of mortality in a whitefish population in northern Lake Huron, estimated total annual mortality rates in excess of 90% for 3-and 4-year-olds. Causes other than fishing accounted for most of the mortality, and predation by lampreys was considered the most probable major source of natural mortality.

The evidence at hand clearly indicates that whitefish populations in Lake Huron are now enduring extremely high mortalities. One consequence is that year classes of whitefish are making their major contributions to the fisheries at successively younger ages. The 1957 year class passed through the Lake Huron fishery at age III and the 1958 year class entered this fishery at age II (Budd and Cucin 1962). The Georgian Bay fishery during the late 1950's was dependent upon age groups VI through X, whereas in the early 1960's the bulk of the catch consisted of age groups IV to VI (Cucin and Regier (1966). Whether or not whitefish populations can continue to thrive in Lake Huron when the brood stock is restricted to one or two year classes is not yet known.

HISTORY OF THE FISHERIES

Development of the commercial fisheries

Archeological evidence indicates that man has used the fishery resources of the Great Lakes for thousands of years. The first European explorers noted that fish was an important item of food to most of the tribes native to Canada. Aboriginals fished with spears, copper fish hooks, fish traps, and gill nets made from materials such as the inner bark of willow and cedar roots. The remains of fish caught 2700 years ago, as dated by the radio carbon technique, have been discovered in the vicinity of Port Franks, near the southern end of Lake Huron (Kennedy 1966).

The earliest settlers caught and used local fish. By 1800 there was a sizeable settlement in the vicinity of Michilimackinac and a local trade in fish. In the early days settlers' wives unravelled linen cloth brought from Europe for clothing and used the threads to make the web of the early gill nets. Before long, however, twine for nets was being imported from Scotland (Kennedy 1966).

About 1831, a Canadian seine net fishery was established in the area of the Fishing Islands, off the west shore of the Saugeen Peninsula. The fish caught in the vicinity were chiefly whitefish and ciscoes. The fish were preserved by salting them in barrels. Approximately 3000 barrels annually were sold to the United States through the port of Detroit (Landon 1944).

A commercial gill net fishery in which cotton or linen mesh was fished from canoes or small boats was begun in Georgian Bay about 1834 (Cucin and Regier 1966). The Bay fishermen at first were mainly voyageurs from Penetanguishene and Indians. The catch was for local consumption or was salted and sold to fish dealers operating with small vessels (Barry 1968). By 1850, production amounted to about 1000 barrels annually. Catches were transported by schooner at the end of the fishing season, and marketed in the United States (Anonymous 1964a). The fishery increased considerably, particularly in southern Georgian Bay, following the arrival of the railway at Collingwood in 1855. Barry (1968) noted a statement from one of John Disturnell's guidebooks, "immense quantities of fish are taken in the waters of Nottawassaga [sic] Bay, being principally carried to the Toronto market," and he quoted an estimate of the value of the catch at about 140,000 per year. Steam tugs were introduced between 1870 and 1875 and the steam gill net lifter about 1890. By the turn of the century, the major innovations in the mechanization of the fisheries had been developed. The fishing effort by the three major gear types in the Canadian waters of Lake Huron during 19 15-65 is shown in Fig. 8.

The total gill net effort has fluctuated between 1.6 and 3.0 million meters, averaging about 2.2 million meters per year since 1915. Nylon gill nets were first fished in 1950 and the change from cotton and linen to nylon was essentially completed in 1953.

Pound nets were first fished in the Canadian waters of Lake Huron in the early 1880's. By 1885, the fishing effort consisted of 70 nets, most of which were located in Georgian Bay and the North Channel-only 8 were in Lake Huron proper (Anonymous 1886). Fishing effort by pound nets reached a peak of over 300 nets in the early 1930's and has declined steadily since that time (Fig. 8). Since 1963, several trap nets have been licensed (Cucin and Regier 1966). The "deep trap net" (Van Oosten et al. 1946) was apparently never used in Georgian Bay.

Night lines (baited hooks) were first used by commercial fishermen on the Canadian side of Lake Huron after the turn of the century. By 1915 the fishing effort on Lake Huron proper consisted of 5000 baited hooks. This level increased to 60,000 hooks by 1925, then decreased gradually to an insignificant effort by 1960.

On the United States side, gill nets appeared near Alpena, Michigan, about 1835, and became widespread in the deeper open waters of the lake within the next 15 years. Lake trout and whitefish were the main species caught with gill nets, although yellow perch, *Perca flavescens,* and white suckers, *Catostomus commersoni,* were taken in the southern portion of the lake. Seines were introduced in the U. S. waters around 1841 and used for taking suckers and walleyes in the Pine and Au Sable Rivers. After the introduction of European carp, *Cyprinus carpio,* to North America in the 1870's (MacCrimmon 1968) seines came into intensive use for carp production in the Saginaw Bay area. Fyke net fishing was carried on in the Saginaw River through the ice for yellow perch, suckers, and catfish. Pound nets were first

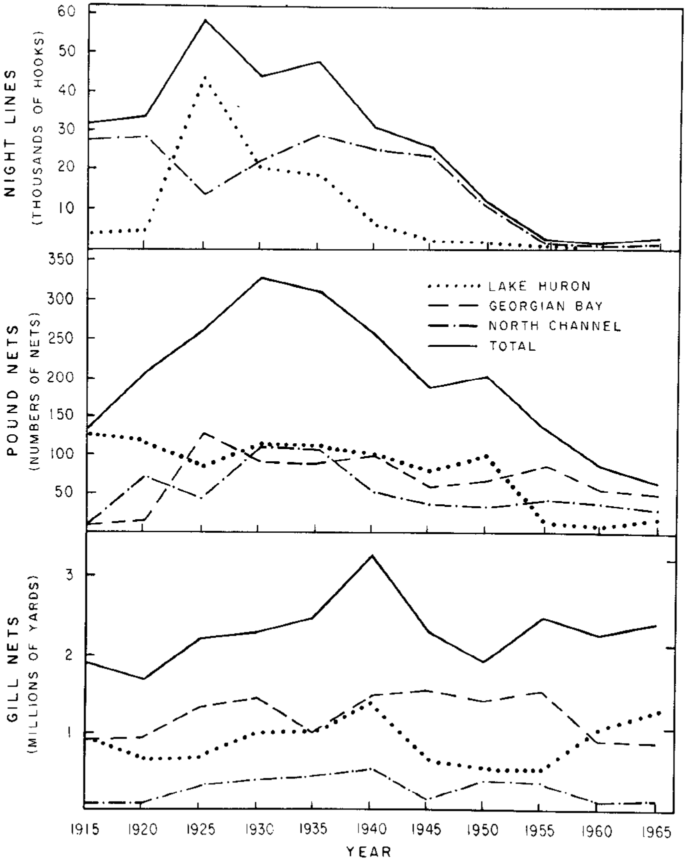

Figure 8. Fishing effort by gill nets, pound nets and night lines in the Canadian waters of Lake Huron from 1915-65. (See Baldwin and Saalfeld 1962, for sources of Canadian statistics).

set in 1854 off Alcona County, Michigan, and by 1860 they were used in all the principal fishing areas on the U. S. side as far north as the Straits of Mackinac (Van Oosten, 1940). Of 428 pound nets in use in U. S. waters in 1885 (Smith and Snell 1891) about 74% were fished in Saginaw Bay. Trap nets were introduced to Lake Huron and fished in Saginaw Bay, and off Iosco and Alpena counties and the St. Marys River by the late 1890's (Van Oosten 1940). The deep water trap net, a larger version of the conventional trap nets, was introduced in 1929. This gear was extremely efficient in taking whitefish and its use was limited by regulation in 1935.

Commercial production

Lake Huron has supported a commercial fishery since the late 1800's and ranks third among the Great Lakes in commercial fish landings. The Canadian fishery is divided among three main areas-including Georgian Bay,

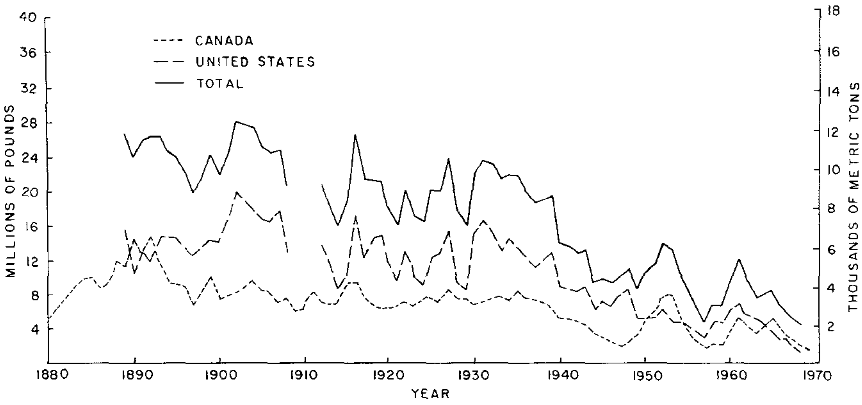

Figure 9. Total production of all species of commercial fish from Lake Huron.

the North Channel, and the open lake. On the United States side, the fishery is located in the lake proper and in Saginaw Bay. Commercial fish production in Canadian waters rose rapidly in the latter half of the last century and reached its maximum of 6000 metric tons per year about 1892; U. S. production reached its peak (9000 tons) at the turn of the century (Fig. 9).

Landings of lake sturgeon, *Acipenser fulvescens,* regarded as a nuisance species because of its destructiveness in the nets, declined from 250 metric tons in 1889 to insignificant levels by 1909 (Anonymous 1969). Carp production increased to over 500 tons by 1917.

From the early 1900's until the mid-1930's, annual production was nearly constant. In the late 1930's, lamprey predation was evidenced in the drop of whitefish, lake trout, and sucker landings, and an almost steady decline in total production continued through 1966. Accompanying this decline was an increase in the proportion of lower valued species such as chubs and yellow perch, in the commercial catch (Smith, S. H. 1968).

The dramatic changes in the fishery from 1940-66, as evidenced by the decline in total catch from 6600 to 3800 tons, was due mainly to the collapse of the lake trout and cisco populations (Figs. 10, 11). Other species, however, including whitefish, sucker, sauger *(Stizostedion canadense),* and walleye also declined during these years. The drop in fish production in Saginaw Bay at this time was attributed to the abandonment of the pound net fishery, rather than to a decrease in abundance of fish (Hile and Buettner 1959). The increased production of chubs (Fig. 12) in U. S. and Canadian waters, from about 250 metric tons in earlier years to 2500 tons in 1961, and the carp catch of 680 tons in 1965 did not compensate for the loss of lake trout and ciscoes (Beeton 1969).

Before 1940, lake trout landings from Lake Huron had fluctuated between 1800 and 2700 tons (Fig. 10). Production first declined in the main body of the lake, then in Saginaw and Georgian Bays. Lake trout production was insignificant in U. S. waters by 11946 and in Ontario waters by 1955. Fry (1953) documented the final decline of the lake trout in South Bay with the

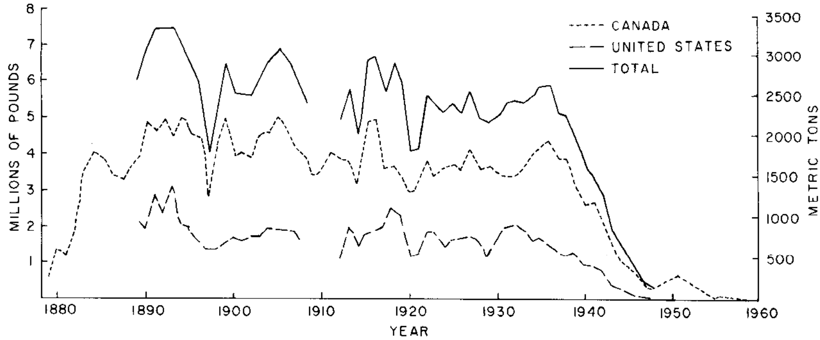

Figure 10. Commercial production of lake trout from Lake Huron.

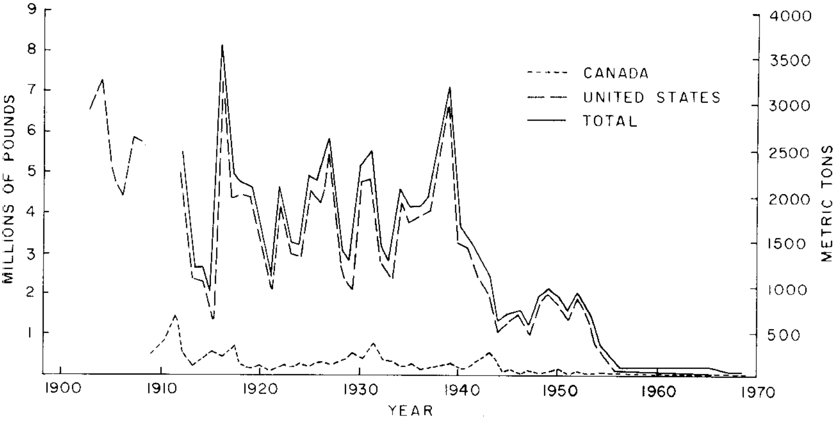

Figure 11. Commercial production of ciscoes from Lake Huron.

passing of the 1944 year class. Tomkins (MS 1951) presented data which show that the increase in production which occurred in Georgian Bay (Fig. 10) was based on that same year class. Only two small lake trout populations have survived, one in McGregor Bay (46'01' N, 81°43' W) (Deyell MS 1967) the other in Parry Sound (45°21'N, 80°06'W) (C. Douglas, personal communication). Why these populations persisted is not known but we suggest that lamprey induced mortality was not critical in these areas because they were isolated from major lamprey concentrations in Georgian Bay. We note that lake trout in South Bay declined several years later than populations in the lake proper.

The decline of the lake trout fisheries in U. S. and Canadian waters of Lake Huron was associated with a number of biological and economic factors, including predation by lampreys, instances of overfishing, deterioration of water quality, and a reduction in the abundance of burbot, *Lota lota*. However, the sea lamprey was the single critical factor in the final decline of

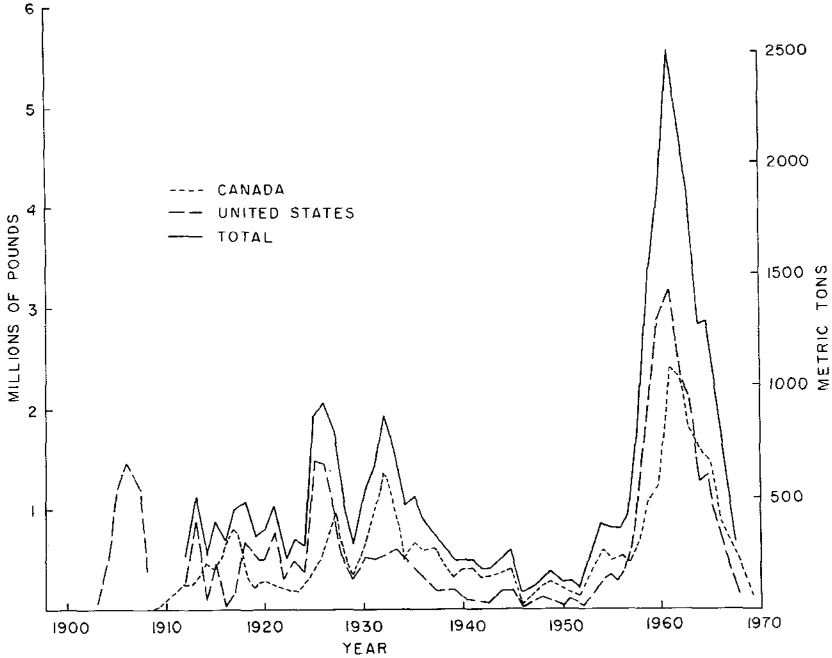

Figure 12. Commercial production of chubs from Lake Huron.

the lake trout in Lake Huron. This conclusion was supported by Fry (1953), Moffett (1958), Baldwin (1968), and Lawrie (1970). Moffett (1958) pointed out that the lake trout populations collapsed progressively from lake to lake in order of their distance from the Welland Canal, the point of entry of the sea lamprey into Lake Erie and the upper Great Lakes. The extreme vulnerability of the lake trout population to lamprey predation is suggested by the relatively low abundance of sea lampreys in all three of the upper Great Lakes at the times when the respective trout stocks started to decline (Fig. 13).

Cisco catches, which amounted to 1400 to 2700 tons per year (Fig. 11), ranked second to those of lake trout in the Lake Huron fishery, from the late 1800's until 1940. Most of this production came from the U. S. fishery in Saginaw Bay; catches from Canadian waters have been relatively small, seldom exceeding 20% of those from U. S. waters in any year. The decline and collapse of the cisco fishery of Lake Huron in 1940-55 followed that of the lake trout in U. S. waters by about 10 years. Beeton (1969) suggested that changes of the environment (eutrophication) in Saginaw Bay, the principal cisco producing area, may have been responsible. However, the cisco also declined in Georgian Bay, where environmental changes during the period of the decline were apparently negligible. Catches of ciscoes have remained insignificant in U. S. and Canadian waters since 1956.

Whitefish landings (Fig. 14) fluctuated between 900 and 1400 tons from 1900 to 1930, increased to 2500 tons in 1932, and then declined to 113 tons

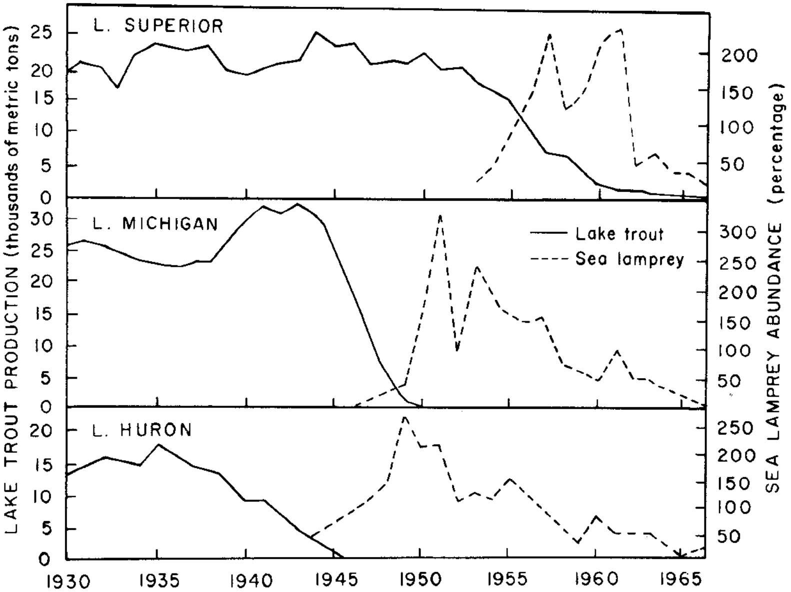

Figure 13. Production of lake trout and abundance of the sea lamprey in the upper Great Lakes. The lamprey abundance index is expressed as a percentage of the average for the period of spawning run counts in each lake. (Data from Smith, S. H. 1968).

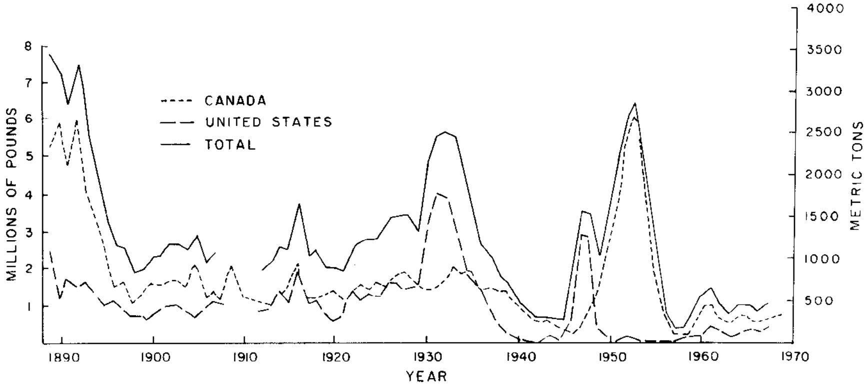

Figure 14. Commercial production of lake whitefish from Lake Huron.

by 1945. This major fluctuation occurred only in U. S. waters, at a time when landings in the Canadian fishery were nearly constant. A second major fluctuation in whitefish production occurred in the U. S. fishery in 194649, and in the Canadian fishery in 1950-56. U. S. catches varied from an insignificant level in 1945 to about 1400 tons in 1947 and Ontario catches from 57 tons in 1945 to a record production of about 2900 tons in 1953. The Ontario whitefish production was based largely on catches from Georgian

Bay, and U. S. catches were mainly from Saginaw Bay. Hile and Buettner (1959) and Lawler (1959) showed that these fluctuations in production were the result of an exceptionally strong 1943 year class. This year class made a substantial contribution to the whitefish production in the North Channel, and probably accounted for the increase in reported landings from a low of 11 tons in 1946 to a high of 140 tons in 1950. Cucin and Regier (1966) confirmed the importance of the 1943 year class in the large catches from Georgian Bay and attributed the 5-year lag in peak landings, after those in the open lake, to a relatively slower growth rate. Budd et al. (MS 1963) suggested that part of the increased catch resulted from an increase in effective effort due to a change from cotton and linen to nylon gill nets. McCombie and Fry (1960) showed nylon nets to be about three times as efficient as cotton with respect to weight of whitefish taken. The increased whitefish production in both the U. S. and Canadian fisheries in 1960 occurred mainly in Lake Huron proper and was attributed by Budd and Cucin (1962) to 2- and 3-year-old fish of the 1957 and 1958 year classes. Production from the 1958 year class was substantial in Georgian Bay (Cucin and Regier 1966). This stock made its major contribution to the fishery at age V in 1963.

Chub landings from Lake Huron (Fig. 12) varied from about 225 to 900 metric tons between 1910 and 1945. Production was generally below 225 tons from 1940 to 1953, the period of the final decline of lake trout. In 1956, exploratory fishing by the U. S. Bureau of Commercial Fisheries indicated the availability of relatively large numbers of chubs (Anonymous 1958); the dissemination of information about these stocks resulted in a greater fishing effort on the chub population. In 1957-61, the total annual production of chubs from the U. S. fishery rose to a record level of 1270 tons. Landings from Canadian waters also increased rapidly during the same period, and reached a peak of 1000 tons in 1961. Chub catches from both fisheries have declined rapidly since 1961, however, and these populations now appear to be on the verge of collapse (Smith 1970).

Sport fisheries

A substantial sport fishery for lake trout existed in Georgian Bay during the early 1900's. This fishery was concentrated in southern Georgian Bay in the vicinity of Parry Sound and along the east side of the Bruce Peninsula. The lake trout were taken mainly in offshore waters by trolling with copper lines from charter boats. A similar fishery for lake trout existed in Michigan offshore waters north of Alpena. These fisheries came to an end with the final collapse of the lake trout populations in the early 1940's.

Little is known about the early sport fisheries in inshore waters, but today substantial fisheries exist for smallmouth bass *(Micropterus dolomieui),* yellow perch, walleye, and northern pike (Esox lucius), in Canadian and U. S. waters. Locally important fisheries for rainbow trout (Salmo *gairdneri)* have developed in the vicinities of river mouths in southern Georgian Bay, off Manitoulin island, and (in U. S. waters) along the northwestern shore of Lake Huron proper.

Artificial propagation and regulation of the fishery

Decreases in fish stocks in the Great Lakes were evident as early as 1871 (Milner 1874). Smiley (1882) attributed decreases in the average sizes of whitefish and lake trout to overfishing. The deterioration in fish populations stimulated interest in artificial propagation and restrictive legislation to prevent further depletion of the resource,

By 1880, two hatcheries were operated in Michigan by the U. S. Commission of Fish and Fisheries, one at Northville and the other at Alpena. The combined production of these stations was about 1 million eyed eggs and yolk sac fry annually. Eggs for incubation were obtained from various whitefish grounds, including the Thunder Bay and Alcona areas of Lake Huron and North Bass Islands in Lake Erie. Most of the fry were shipped by specially equipped railroad cars to various ports along Lake Huron and Lake Erie, and planted along the coasts (Anonymous 1885). Whitefish propagation continued at the Northville hatchery until recent times (Regier et al. 1969).

On the Canadian side of Lake Huron, hatcheries were built by the Federal Government at Sarnia and Wiarton in 1908 and at Southampton and Collingwood in 1912. At Sarnia, the hatchery was equipped with jars and troughs for a combined trout and whitefish operation. The Wiarton and Southampton hatcheries were designed exclusively for lake trout, and the Collingwood hatchery, for the care of eggs and fry of whitefish, cisco, and walleye. In 1933 a jar-type hatchery was built by the Province of Ontario at Little Current on Manitoulin Island, for the propagation of eyed eggs and fry of whitefish, cisco, and walleye. The stocks produced were intended to supplement natural reproduction in the North Channel and to provide walleye fry for introduction into small inland waters.

In U. S. waters of Lake Huron before 1933, closed seasons were enforced during the spawning seasons for lake trout and whitefish and spawn for the hatcheries was obtained by limited commercial fishing under special permits during the closed season. Since 1933, closed seasons have been strictly enforced for the various species of commercial fish, although spawn collected during the open season has been incubated at the hatcheries (Van Oosten 1937b). Eggs for incubation in Canadian hatcheries were salvaged from the catches of commercial fishermen who were permitted to fish on the spawning grounds through the respective spawning seasons.

The confidence of government agencies in the success of the early hatchery programs was shared by the general public, as well as by commercial fishermen and anglers. The statements by Keyes (1894) and Post (1894) that the large plantings of whitefish were not producing the expected results were apparently disregarded. Local increases in abundance of whitefish were ascribed by Clark (1885), McDonald (1909), and Reighard (1910) to hatchery plantings. Increased emphasis was placed on artificial propagation as the foundation of fisheries management. By the turn of the century, the total Federal (U. S.) production of eggs, fry, and fingerlings exceeded 1 billion, and continued to increase to a peak of 7 billion by 1928 (Wood 1953).

In spite of the intensive planting program in the Great Lakes in the late 1800's and early in this century, the catches of whitefish, the species of greatest interest to fish culturists, continued to decrease. Koelz (1926) suggested that hatchery programs may have been deleterious to the fishery by fostering the view of the fishermen that the protection of spawning fish was unnecessary as long as fish propagation continued. It is also possible that the deliberate redistribution of progeny of stocks from one lake to another (especially the widespread distribution of Lake Erie whitefish eggs and fry) served to destroy racial distinctions in the native populations. Various forms of lake trout (including siscowet) and whitefish recognized by Georgian Bay fishermen, apparently disappeared long before the final decline of the trout in Georgian Bay (Anonymous 1893).

During the 1930's results began to accumulate of statistical comparisons of whitefish plantings with production data. Hile (1937), Van Oosten (1942), Carlander (1945), Miller (1952), Lapworth (1956), and Christie (1963) all failed to find significant correlations between the numbers of fry planted and production and abundance in the years when the resulting fish would have been vulnerable to commercial fishing gear. Due to lack of evidence of any significant contribution of hatchery plantings to commercial fisheries in the Great Lakes and the difficulty in obtaining sufficient quantities 'of eggs, the hatcheries were closed.

In Canada, the Southampton hatchery closed operations in 1953, Sarnia in 1954, Collingwood in 1957, and Little Current in 1967. Although the propagation of Lake Huron lake trout ceased in 1954 at Wiarton due to the final collapse of the Georgian Bay population, the hatchery has continued to hatch lake trout eggs from lakes Manitou and Simcoe, and, recently, eggs of kokanee salmon, *Oncorhynchus nerka,* from British Columbia. At present, brood stocks of fourth and fifth generation splake are being maintained in the Chatsworth and Tarentorus hatcheries (Ontario) and the Marquette hatchery (Michigan) for the purpose of producing yearling hybrids for the rehabilitation of the trout fishery in Lake Huron.

Introductions of exotics

Of the deliberate and accidental introductions of exotics in the upper Great Lakes, only that of the rainbow trout has been an unqualified success. Probably the accidental introduction of the sea lamprey has been the most seriously detrimental; it has resulted in a severe and long term depression in the fishing economics of the upper Great Lakes.

Rainbow trout.-The rainbow trout was the first exotic introduced to Lake Huron. This species, native to the Pacific coast of North America, was introduced to Lake Superior by the U. S. Fish Commission in 1895 (MacKay 1963). According to Radforth (1944) the first authenticated record of rainbow trout in Lake Huron was a 1.8 kg fish caught off Duck Island, south of Manitoulin Island, in 1904. By 1930 spawning populations of rainbow trout were established in most major tributaries of Lake Huron, with the exception of those draining the Precambrian Shield. Rainbow trout in Lake Huron usually spawn in April and May, although their spawning period may extend over several months (Dodge and MacCrimmon 1970). They spawn in gravel deposits of tributary streams. After spawning, most adults return to the lake. The young remain in their natal stream for up to 2 years before migrating to the lake. Sexual maturity for both sexes of rainbow trout in

Lake Huron tributaries is attained as early as age III (Dodge and MacCrimmon 1970).

Rainbow trout have been classed as a game fish since their introduction to the Great Lakes, hence their abundance is not reflected in commercial production statistics. Important sport fisheries for this species have developed in both the Canadian and U. S. waters of Lake Huron. In spite of substantial predation on rainbow trout in Lake Huron by the sea lamprey (Berst and Wainio 1967; Dodge and MacCrimmon 1970), these populations have persisted. The diet of immature rainbow trout in streams consists mainly of aquatic and terrestrial invertebrates. Larger fish (in the lake environment) are essentially piscivorous (MacKay 1963).

Brown trout.-This species *(Salmo trutta)* was introduced into North America from Germany with a planting of fry in the Pere Marquette River, a tributary to Lake Michigan, in 1883. Small naturalized populations of the species occur in river systems tributary to Lake Huron (MacCrimmon and Marshall 1968).

Carp.-The initial plantings of this species were made in the United States as early as 1831. Between 1880 and 1893 several lots of carp were sent by the U. S. Fish Commission to applicants in Ontario, including the Ontario Fish and Game Commission (Dymond 1955). They were introduced into Lake Erie in 1883 and were present at the entrance to the St. Clair River as early as 1900. They were first observed in Georgian Bay in 1905 and by 1914 had been recorded in a commercial catch from the North Channel. Carp are now distributed throughout the littoral waters of Lake Michigan. During the spring the fish migrate from the deeper water of the Great Lakes into marsh areas to spawn. Adults are in the epilimnion during the summer months, occupying marginal areas of deeper water during the late summer and early fall, and move into deeper water and remain there during the winter (MacCrimmon 1968).

Smelt. -Smelt *(Osmerus* mordax) were first introduced successfully into the upper Great Lakes by a planting in Crystal Lake, Michigan, in 19 12. They were first reported in Lake Huron in 1925 and increased sharply in the 1930's (Van Oosten 1937a). In the Great Lakes they inhabit waters 14 to 64 m deep and are most abundant in the 18-36 m zone. The adults move inshore and congregate in dense schools in April prior to spawning. They feed on invertebrates until they reach a length of about 15 cm; other fish (including smelt) are then added to the diet (Van Oosten 1953).

Alewives. -Alewives *(Alosa pseudoharengus)* were unknown in the Great Lakes before 1873, when they were first recorded in Lake Ontario. Fifty-eight years elapsed before the alewife was recorded in Lake Erie. They were first found in Lake Huron in 1933, Lake Michigan in 1949, and Lake Superior in 1954 (Smith 1970). From their first appearance in South Bay of Lake Huron in 195 1, they increased steadily in abundance until 1964 when almost 200 tons were taken in experimental nets (Coble 1967). They have subsequently undergone an irregular decline in South Bay.

Dense schools of alewives occupy the various depths of Lake Huron during different seasons. Young alewives are at intermediate depths of the lake during fall and winter. Adult alewives move from deep water towards shore in late winter and early spring, and spawn near shore in rivers and bays during

June and July (Wells 1968). Alewives feed on plankton, aquatic insects and crustaceans (Scott 1967).

Sea lamprey.-The sea lamprey has probably been present for many centuries in Lake Ontario, where it is still abundant. It was first reported in Lake Erie in 1921 (Dymond 1922) and in Lake Huron in 1937 when a spawning run was observed in the Ocqueoc River, Michigan (Applegate 1950). The life history of the sea lamprey in the Great Lakes includes a larval existence of about 4 years (including transformation of ammocoetes to the parasitic form) in silt beds of tributary streams, and a subsequent parasitic life of 12 to 18 months in the lakes. Parasitic life is terminated by a spawning migration beginning in early April and continuing until mid-June. Adults die after spawning (Applegate 1950). Lampreys reached their greatest abundance in Lake Huron about 1948, and then declined steadily; by 1965 abundance was less than 10% of that in the late 1940's (Fig. 13). This reduction occurred before a significant chemical control program had been started.

Predation by sea lampreys drastically reduced populations of large cold-water fishes, including lake trout, burbot, whitefish, and rainbow trout. The threat of destruction of valued fish stocks by this predator stimulated research into control methods. Efforts to control lampreys in the upper Great Lakes have included the use of mechanical and electrical barriers on spawning tributaries (Baldwin 1968) and the development and application of a selective toxicant, 3-trifluoromethyl-4-nitrophenol (TFM), for the elimination of ammocoetes from their natal streams.

Splake.-First generation splake were planted in Lake Huron by the Province of Ontario during the 1950's and 1960's (Berst and Spangler 1970). These fish tended to remain in the general vicinity of the planting sites. Smelt and sticklebacks, *Pungitius pungitius,* were important in the diet of yearling splake, whereas older hybrids fed mainly on smelt and alewives. The hybrids grew rapidly in Lake Huron (Fig. 6) and the onset of sexual maturity in the hybrids occurred at age II when the fish were not completely vulnerable to lampreys and commercial fishing gear. Even when the hybrids were completely vulnerable, at age III, a small number survived through the spawning season.

The first plantings of F_4 and F_5 splake, selected for early maturity and the ability to occupy deep water, were made in 1969. These plantings are part of a joint program of rehabilitation of the trout fishery of Lake Huron by the Province of Ontario and the State of Michigan, coordinated by the Great Lakes Fishery Commission. Because of the early maturity, it is expected that the hybrids will surpass the native lake trout in their potential to develop self-sustaining populations in the presence of exploitation by the fisheries and residual lamprey populations.

Kokanee salmon.-Kokanee salmon were first introduced to Lake Huron with a planting of 277,100 eyed eggs by the Ontario Department of Lands and Forests in the fall of 1964. Since 1965, over 5 million eyed eggs, fry, and fingerlings have been planted in Lake Huron. Natural reproduction of kokanee has been observed in streams tributary to Lake Huron, but whether self-sustaining populations will be established is still unknown (Collins 1971).

Coho salmon.-Coho salmon, *Oncorhynchus kisutch,* first appeared in Lake Huron in 1967, following plantings of 660,000 yearlings in Lake Michigan in 1966. Mature coho salmon were transplanted to several tributaries of Lake Huron in 1967 (Ricker and Loftus 1968). During 1968 and 1969, plantings in excess of 1 million yearlings were made in Lake Huron tributaries. Large numbers of salmon moved from the planting sites in Michigan waters to the Canadian side of Lake Huron proper. In 1969 a total of 40 tons of this species was taken in the Canadian commercial fishery in lower Lake Huron (R. Payne, personal communication).

Chinook salmon.-Chinook salmon, *Oncorhynchus tshawytscha,* were first introduced to Lake Huron by the State of Michigan in 1969 (Smith, S. H. 1968) and plantings through 1971 totalled 1.3 million yearlings.

DISCUSSION

The present depressed state of valued fish stocks in Lake Huron is the result of a series of changes which were underway by the end of the 19th century. The general decline which has persisted since that time has accelerated markedly during the past 4 decades.

Limnological conditions in Lake Huron have changed only slightly since the 1800's. Lake Huron is today as it was then, a deep oligotrophic lake. The only significant changes are confined to areas adjacent to centers of human activity, chiefly inner Saginaw Bay and various harbours and estuaries in Georgian Bay. Levels of total dissolved solids have increased less than 5% since the early 1900's in Lake Huron, whereas they have increased about 15% in Lake Michigan and about 40% in the lower lakes. The increase for Lake Huron must have been insignificant in the major water masses although shoreline areas have been more seriously affected.

Recent events, the significance of which are not yet understood, include thermal pollution and increased levels of chlorinated hydrocarbons and heavy metals such as mercury. The vulnerability of the important fish stocks in Lake Huron to these changes is related to the degree of their dependence upon the littoral zone. We submit that physically or chemically toxic effluents which can be concentrated by prevailing onshore winds or by thermal bars could jeopardize the survival of the early life stages of whitefish, ciscoes, and trout. The most notable example of the adverse effect of eutrophication on fish stocks of Lake Huron is in inner Saginaw Bay. Beeton (1969) concluded that the: dramatic decline in sauger, walleye, and whitefish populations in Saginaw Bay indicates a deterioration of the environment since 1935 to the extent that it is no longer suitable for these species.

Since it is apparent that environmental deterioration has played only a minor role in the decline of fish stocks in Lake Huron proper, other hypotheses have been proposed to account for the continuing decline of valued stocks. There is little doubt that overexploitation was the cause of the near extinction of the sturgeon in Lake Huron. Direct evidence from Lake Huron on this point is not available, but Regier et al. (1969) stated the case adequately for all of the Great Lakes. Van Oosten et al. (1946) attributed the collapse of the whitefish fishery in the U. S. waters of Lake Huron to the use of the deep-water trap net, which was introduced to U. S. waters in 1928 at a time when whitefish abundance was high. This gear, which was never fished in Canadian waters, was used extensively throughout U. S. waters of Lake Huron by 1930. As the nets were moved successively into various sections of the lake, local stocks were depleted rapidly. The U. S. catch declined from 1860 metric tons in 1931 to 860 tons in 1935, when restrictions were imposed that prohibited setting trap nets in water deeper than 24 m. The whitefish catch continued to decline to less than 45 tons in 1942. We attribute this decline to the continuing intensive fishery for lake trout which exploited whitefish as an incidental species. The whitefish stocks in Georgian Bay showed no marked change in production during the decade of the 1930's.

The smelt populations in Lake Huron established themselves during the 1920's. These populations underwent a population explosion in the late 1930's and early 1940's. During this period, production of lake trout, whitefish, ciscoes, and chubs began a major decline. In the winter of 1942-43 the smelt population of Lake Huron collapsed. The following spring saw the emergence of the greatest year class of whitefish ever recorded for Lake Huron. Ciscoes reversed their precipitous decline and from the mid-1940's until the early 1950's, annual production of this species was relatively stable at 1000 to 1500 metric tons. It is obvious that the larger smelt populations prior to 1942 were utilizing vast quantities of food organisms near the base of the production pyramid. We suspect that in the virtual absence of the smelt population following the die off of 1942-43, populations of whitefish and ciscoes may have capitalized on this large reservoir of available energy.

Alewives were considered by S. H. Smith (1968) to have been associated with the decline of the deep-water coregonines in Lake Michigan because of their intensive utilization of invertebrate food in various zones of the lake. We agree that alewives have probably had a considerable influence on the Lake Huron fish community in recent years, but the major changes in commercially important species occurred well before alewives became a prominent component of the fauna. We consider the recent abundance of alewives a symptom rather than a cause of instability in the community of native species.

If any one factor can be singled out as having played a leading role in the impairment of the Lake Huron fisheries, it must have been the sea lamprey. The natural species complex in Lake Huron was based on a deep-water coregonine community which supported the high level carnivores (including the lake trout and burbot) and the commercial fishery. The extinction of the lake trout and the decline of the burbot led to a dramatic succession of changes in the populations of other species (Smith, S. H. 1968). Distribution of energy among the chub populations shifted to the smaller species as the larger chubs were selectively removed by an exploding lamprey population and a commercial fishery which had no premium species to exploit. Generations of lampreys in tributary streams, produced by adults which had fed extensively on lake trout, burbot, and large chubs, emerged from their natal streams at a time when stocks of large fish were severely depressed. These lampreys utilized such remaining species as whitefish, ciscoes, and suckers, thus releasing food resources for utilization by forage species too small to fall prey to lampreys. Smelt, alewives, and deep-water chubs swiftly attained a dominant position in Lake Huron during the late 1950's and early 1960's. The differences, apparent in Table 1 between yield during the periods of 192340 and 1941-60, undoubtedly reflect the diversion of fish production from the commercial fishery to the sea lamprey and other low valued species.

Although lake trout in the major basins of Lake Huron were exterminated by lampreys, other large species such as rainbow trout, whitefish, white suckers, and burbot have persisted. These species share a relatively early sexual maturity, spawning initially by age III. Rainbow trout have an additional advantage due to a reduced availability to lampreys during their spring and fall migrations into tributaries.

With the exception of the near extinction of the sturgeon and the decline in the lake whitefish fishery in U. S. waters in Lake Huron following the introduction of the deep-water trap net, we are unable to relate the depleted stocks of native species to over-exploitation by the commercial fisheries. Commercial exploitation must certainly have acted in concert with "exploitation" by sea lampreys, but their independent effects are unknown.

The present instability in the fishery resources of Lake Huron will undoubtedly continue until sea lamprey control is achieved and climax predators are re-established. The first round of chemical treatments of lamprey spawning streams of Lake Huron was completed in 1970. An additional series of chemical applications must begin within the next year or so to prevent the emergence of ammocoetes resulting from lamprey reproduction since the first series of treatments. Efforts by Canadian and U. S. agencies to re-establish predatory species now include the planting of coho and chinook salmon and F_5 splake. In addition, both governments are proceeding toward the establishment of water quality criteria which, it is hoped, will prevent any further deterioration of the aquatic environment.

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