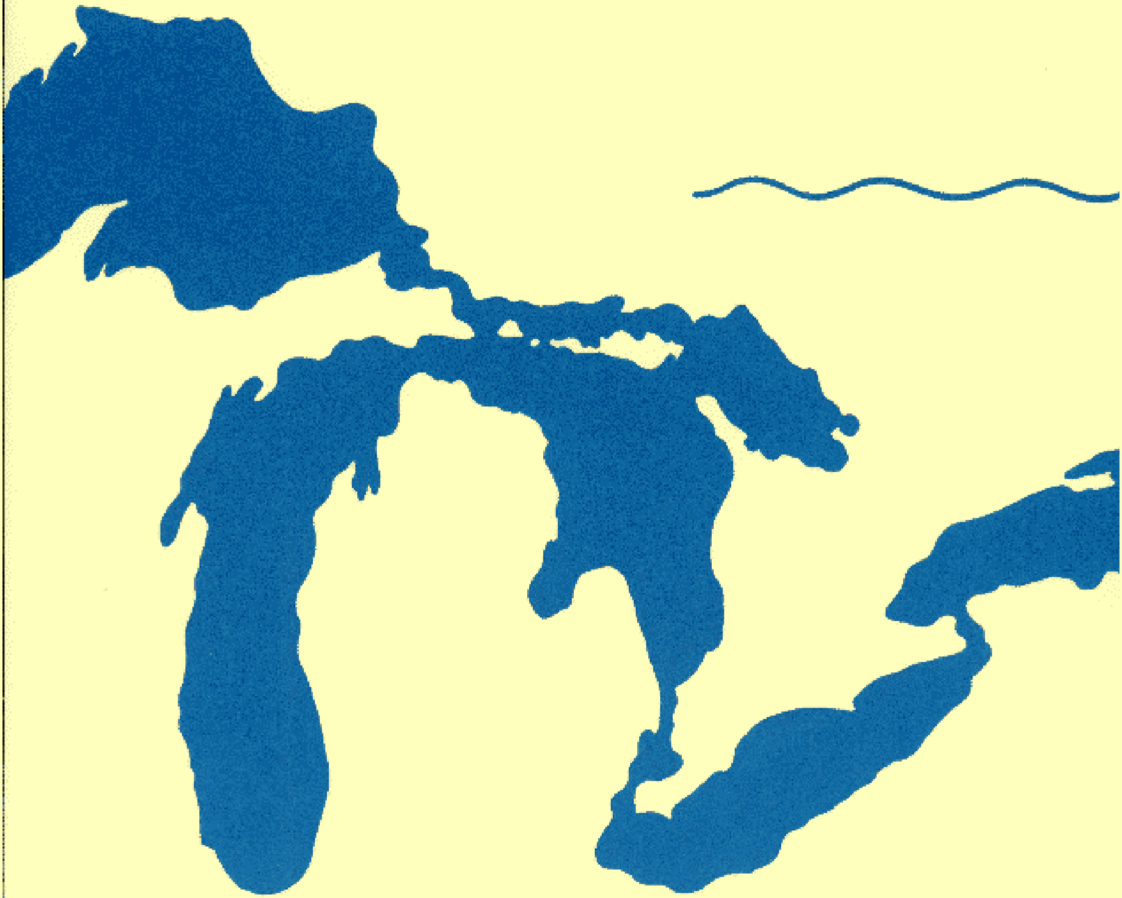
LAKE SUPERIOR

A Case History of the Lake and its Fisheries



Great Lakes Fishery Commission

TECHNICAL REPORT No. 19

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 SUPERIOR
A Case History of the Lake and its Fisheries

by

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TECHNICAL REPORT No. 19

GREAT LAKES FISHERY COMMISSION
1451 Green Road
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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 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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LAKE SUPERIOR

A Case History of the Lake and its Fisheries[1]

by

A. H. Lawrie and Jerold F. Rahrer[2]

ABSTRACT

A general review of current knowledge of Lake Superior and its fish stocks is presented. Relevant information relating to its history, physical and biological limnology, fisheries exploitation, and introductions of hatchery-reared fish is considered. Except for the likelihood that local fluvial or inshore environments were adversely affected by deposits of sawdust and other woody allochthonous materials late in the last century, no evidence was found of a general deterioration in the aquatic environment which could account for the severe depletion suffered by all species of commercially important fish. On the other hand all appear, more or less obviously, to have suffered from some degree of overfishing over a long period. More recently, predation by the sea lamprey (Petromyzon marinus) has had severe effects, both direct and indirect, on many species, especially lake trout *(Salvelinus namaycush)* and lake whitefish *(Coregonus clupeaformis)*. These effects have proven to be at least partly reversible with application of suitable methods of lamprey control and support of affected species from hatchery sources.

INTRODUCTION

Lake Superior lies at the head of the St. Lawrence River drainage, 183 metres (600 feet) above mean sea level and about 2900 kilometres (1800 miles) from the open Atlantic. It is broadly triangular with its apex almost exactly at 49 degrees North, 88 degrees West and its base stretching some 600 km (370 mi) east-west just below the 47th parallel of latitude.

During the exploration and settlement of the continent travel was very largely by water and the St. Lawrence drainage, for obvious reasons, provided the premiere access to the interior of the continent. By the middle of the 17th century all of its Great Lakes had been explored by expeditions from the French settlements about Quebec on the lower St. Lawrence and their general characteristics were known. Early exploration and exploitation of the resources about the lower lakes was inhibited by the hostility of the Iroquois, a confederation of Indian nations whose northern territories just reached those lakes. In contrast, the Ottawa River and the canoe routes through Lake Nipissing to Georgian Bay and Lake Huron offered a direct, relatively secure passage to the upper lakes. In consequence Lake Superior was discovered in

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[2] Deceased.

1616, 24 years before Lake Erie (Lower, 1946; Lanctot, 1963; Thwaites, 1968).

That the lake was cold, of exceptional clarity, and abounded in fish of fine quality was recorded by Father Allouez, a Jesuit missionary, who visited it in 1665 (LeMercier, 1667). This readily available food resource, extensively used by the Indian peoples living along both shores of the lake, was of vital importance to missionary, fur trader, and settler throughout the next century and a half. Commercial exploitation, involving export and sale of the catch beyond the boundaries of the lake basin, began about the turn of the 19th century and has, with minor interruptions, continued until the present day. As the rapid growth of the mid-western U.S. population during that century provided ready markets for the minerals and forest products of the area, settlement of the basin quickened and the fisheries entered upon the phase of expansion and modernization culminating in the intense exploitation, especially in U.S. waters, which characterized the first half of the present century.

Perhaps because the soils and climate are inimical to the development of an indigenous agriculture, the economy of the Lake Superior basin has not progressed much beyond the exploitative phase, and in contrast to the megalopolitan developments about the lower lakes, human population densities have remained low, less than 20 persons per square mile throughout most of the watershed (Fig. 1; Lee and Beaulieu, 1971). In consequence, with some important local exceptions largely associated with mining developments or the few scattered urban areas, the lake has been little affected by either industrial pollution, or enrichment from agricultural or residential sources. No doubt the

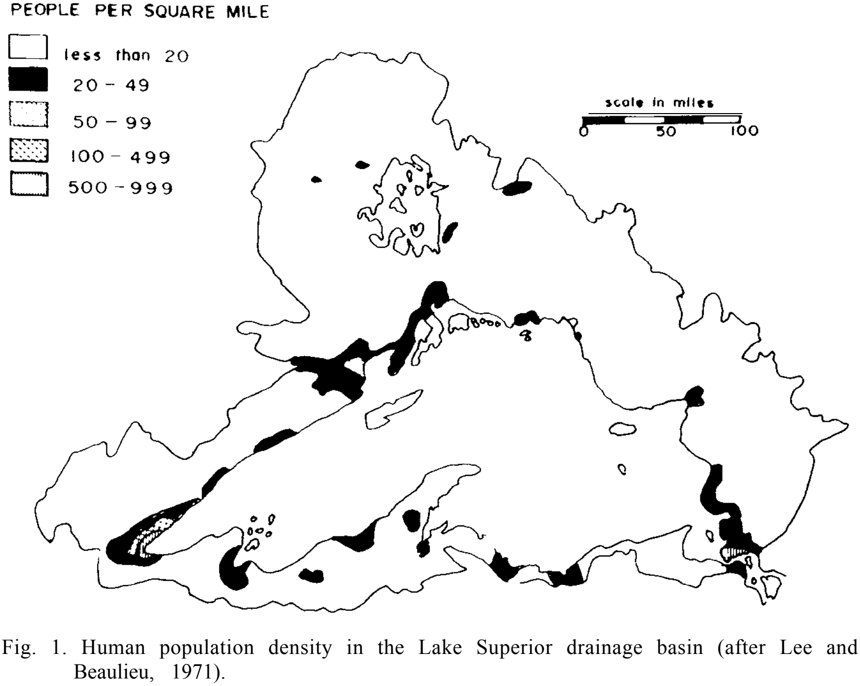

Fig. 1. Human population density in the Lake Superior drainage basin (after Lee and Beaulieu, 1971).

recurrent cycles of cutting and reforestation which have characterized lumbering operations throughout the watershed have had both qualitative and quantitative effects on nutrient input to the basin but available records permit no direct assessment of the importance of this influence. However, since the lake has been universally adjudged to be oligotrophic at the present time (Beeton and Chandler, 1963; Beeton, 1969; Alley and Powers, 1970; Ryder, 1972) it is reasonable to consider any eutrophying influence to have been generally insignificant.

Since the last quarter of the 19th century widespread efforts have been made by government agencies both to introduce new fish species to the lake and to sustain those whose declining abundance was of concern. At various times commercial fishermen, concerned over the apparent depletion of one or other of their target species, have made informal attempts at artificial propagation by returning to the lake fertilized eggs of fish taken during the spawning season. It is not really clear that these activities, formal or informal, have materially affected the populations of any species other than certain salmonids, notably brown and rainbow trout *(Salmo trutta* Linnaeus and *Salmo gairdneri* Richardson), which have become established in the basin as a result of artificial propagation, and lake trout *(Salvelinus namaycush* (Walbaum)), whose depleted populations have been substantially rebuilt by a massive program of planting.

Certain species have extended their range into the lake either by virtue of inadvertent introduction or by passage through the ship canals at the outlet. Conspicuous among these have been the rainbow smelt *(Osmerus mordax* (Mitchill)) and the sea lamprey *(Petromyzon marinus* Linnaeus). The role of the former in the ecosystem is not yet fully understood although there is a growing suspicion that it has interacted in subtle ways with the indigenous populations to their detriment. The latter has been responsible for intense predation upon the larger fish species, particularly upon the lake trout and its associates, resulting in a precipituous decline in fish stocks in the 1950's and terminating the highly exploitive phase of the commercial fishery. This led to the inauguration of intensive programs of sea lamprey control and fisheries management which are still in progress and whose results, though highly encouraging, have yet to be fully assessed.

Thus Lake Superior provides an example of an oligotrophic lake as yet little affected by eutrophying influences which has been exposed to a century and a half of increasingly intense exploitation, followed by unusually heavy natural mortalities generated by an exotic and recently arrived predator, and to increasingly intensive and relevant artificial recruitment from hatchery sources.

THE LAKE AND ITS DRAINAGE BASIN

Morphometry and hydrology

Table 1 displays the principal morphometric and hydrologic data available for the Lake Superior basin. Because the lake is shared subequally by Canada and the U.S., individual values for the two countries have been

Table 1. The morphometry and hydrology of the Lake Superior basin.

Length[a]		668.3 km	350 mi
Breadth[a]		305.5 km	160 mi
Depth		406.3 m	1,333 ft
	mean	148.3 m	487 ft
Shoreline Length[b]	U.S.	1,463.0 km	909 mi
	Can.	1,475.7 km	917 mi
	Total	2,938.7 km	1,826 mi
Surface Area	U.S.	53,613.0 km^2	20,700 mi^2
	Can.	28,800.8 km^2	11,120 mi^2
	Total	82,413.8 km2	31,820 mi^2
Volume		12,233.3 km3	2,927 mi^3
Land Drainage Area[c]	U.S.	43,770.8 km^2	16,900 mi^2
	Can.	101,786.6 km^2	39,300 mi^2
	Total	145,557.4 km^2	56.200 mi^2
Number of Tributaries[d]	U.S.	840	
	Can.	685	
	Total	1,525	
Mean Annual Discharge[c] (1922-1970)		2,124.7 m3/s	75.05 1 cfs
Retention Time		182 years	

[a] In the sense of Hutchinson (1957).

[b] Lee and Beaulieu (1971).

[c] Canada Department of Energy, Mines and Resources. The areas of the Ogoki and Longlac diversions are included in the drainage areas.

[d] Canada Department of Fisheries and Forestry and US. Bureau of Sport Fisheries and Wildlife. Many of these streams are intermittent but do convey runoff to the lake at some time each year.

presented where appropriate. Sources for controversial or original entries are indicated in the footnotes accompanying the table.

Since 1922, in the interests of both navigation and the generation of electrical power, discharge from the lake has been controlled by a compensating dam in association with the navigational locks at the outlet of the lake. The flows through these structures are highly variable both from year to year and from month to month. For the post-control period, 1922-1970, mean annual flows calculated as the average of mean monthly flows have ranged from a low of 1771.5 cubic metres per second (62,576 cubic feet per second) in 1963 to a high of 2623.1 m^3/s (92,655 cfs) in 1952. Individual mean monthly values for this period range from a minimum of 1157.9 m^3/s (40,000 cfs) in September 1955 to a maximum of 3598.2 m^3/s (127,100 cfs) in August of 1943. (Data from the U.S. Army Corps of Engineers through Canada Department of Energy, Mines and Resources courtesy John Bouchard, Canal Superintendent, Sault Ste. Marie, Ontario.)

Lake Superior levels, on the other hand, have been essentially stable. Spectral analyses of mean monthly water levels (Ku, 1970) indicate that annual and semiannual components contribute better than 90% of the water level variations. In addition, Liu (1970) provides evidence of a weak, long term cycle with a periodicity of approximately eight years. The amplitude of the resulting seasonal variation rarely exceeds half a metre (U.S. Fish and Wildlife Service, 1970; Lee and Beaulieu, 1971) and mean annual levels for the two periods 1860-19 13 and 1941-1967 (precontrol and postcontrol) were

182.94 ± 0.20 and 183.06 ± 0.17 m (600.19 ± 0.66 and 600.58 ± 0.56 ft) above mean sea level (Liu, 1970). Since most of the remaining lake dimensions are a function of level they may reasonably be considered to be stable and subject to little seasonal or annual variability.

Because relatively few of the tributaries to Lake Superior have been gauged for any length of time, estimates of runoff from streams influent to the lake cannot be stated with the precision attributed to measurements of levels or outflows. Hence it has been customary to talk in terms of Net Basin Supply, which includes precipitation on the lake surface plus runoff from the drainage basin and any ground water contribution less evaporation from the lake surface, calculated as a single value from the known parameters of the storage capacity of the lake basin, its level, and the outflow (Gburek and Berry, 1967; Carlson and Persoage, 1967; DeCooke, 1968). Recently, however, attempts have been made to estimate the runoff from the drainage basin by plotting unit runoff values at the centroid of the drainage area for those streams which have been guaged, interpolating contours of equal runoff and so constructing a runoff map (Browzin, 1966; Pentland, 1968). Table 2, modified from Pentland, shows his estimates of the mean monthly runoff from the Lake Superior drainage in litres per second per square kilometre and cubic feet per second per square mile. Fig. 2, also adapted from Pentland, demonstrates that runoff is heavier along the south and east shore than it is along the north and west shore as would be expected from the distribution of both snowfall and rain over the basin (Lee and Beaulieu, 1971). The estimates are considered to represent "natural" runoff being based on uncontrolled watersheds exclusively. Since a number of watersheds are controlled for various purposes actual runoff values will be somewhat different from those shown.

The bedrock and glacial geology

Lake Superior lies along the southern edge of the Canadian Shield where its extensive drainage basin straddles both Precambrian and Palaeozoic formations. The lake itself is thought to have formed as a rift valley system in the late Precambrian (Halls and West, 1971) the faulting perhaps resulting from

Table 2. Mean land runoff (1935-64), Lake Superior basin. After Pentland (1968)

Month	litres/s/km^2	cfs/mi^2
January	4.70	0.43
February	3.94	0.36
March	5.90	0.54
April	21.32	1.95
May	29.96	2.74
June	18.15	1.66
July	10.82	0.99
August	**6.56**	**0.60**
September	7.33	0.67
October	8.42	0.77
November	9.29	0.85
December	7.00	0.64

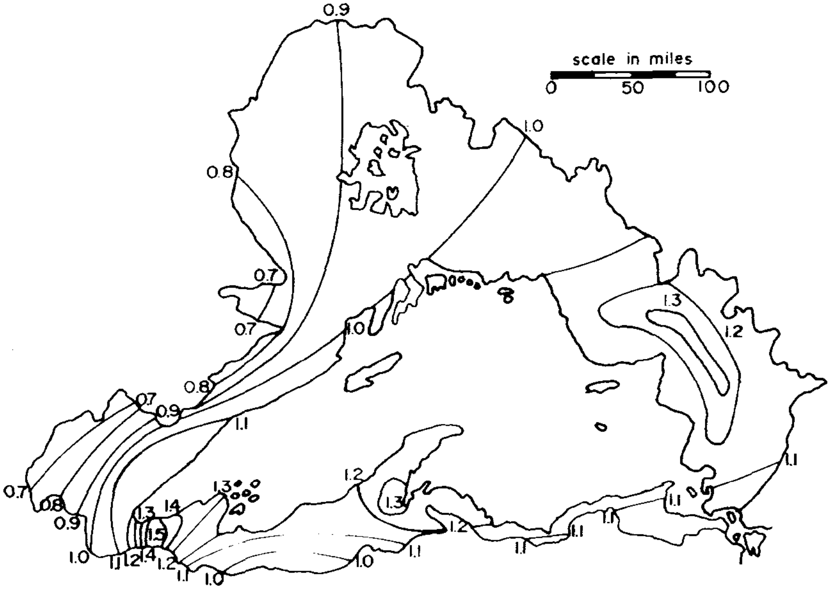

Fig. 2. Mean annual runoff in cfs/mi^2 from the Lake Superior drainage basin (after Pentland, 1968).

the extrusion of enormous volumes of basic lava from beneath the basin during middle Keweenawan time (Pye, 1969).

It has been shown (Halls and West, 1971) that 90% or more of the present lake basin is underlain by the relatively friable red quartzose sandstones of the Bayfield and Jacobsville formation, which are either the last of the Precambrian sediments or the earliest Palaeozoic, Cambrian deposits. Whatever younger beds may have occupied the basin they appear to have been completely scoured out. However, under the east end of the lake where the overlying mantle of glacial drift and modern lacustrine sediments is thin the prominent ridge and valley topography of the bottom has been interpreted as the remnant of a preglacial drainage by Farrand (1969). The bedrock topography of the western basin is similarly rough although this is completely obscured by a heavy mantle of drift. The Bayfield-Jacobsville sediments have little exposure beyond the margins of the present lake, occurring only as a narrow intermittent band along the south shore and the extreme southern end of the east shore (Fig. 3).

Except for a few outliers further west unquestioned Palaeozoic rocks enter into the drainage basin of the lake only south of its eastern third, where outcrops of upper Cambrian sandstones, middle and upper Ordivician and lower middle Silurian shaly limestones and dolomites are successively encountered in passing southward from the lake shore. Elsewhere, except for the earlier noted Bayfield-Jacobsville sandstones, the drainage basin rests wholly on the Precambrian rocks of the Southern and Superior Provinces of the Canadian Shield (Stockwell et al., 1971).

The Superior Province invests virtually the entire eastern half of the north shore and extends far beyond the limits of the drainage basin to the

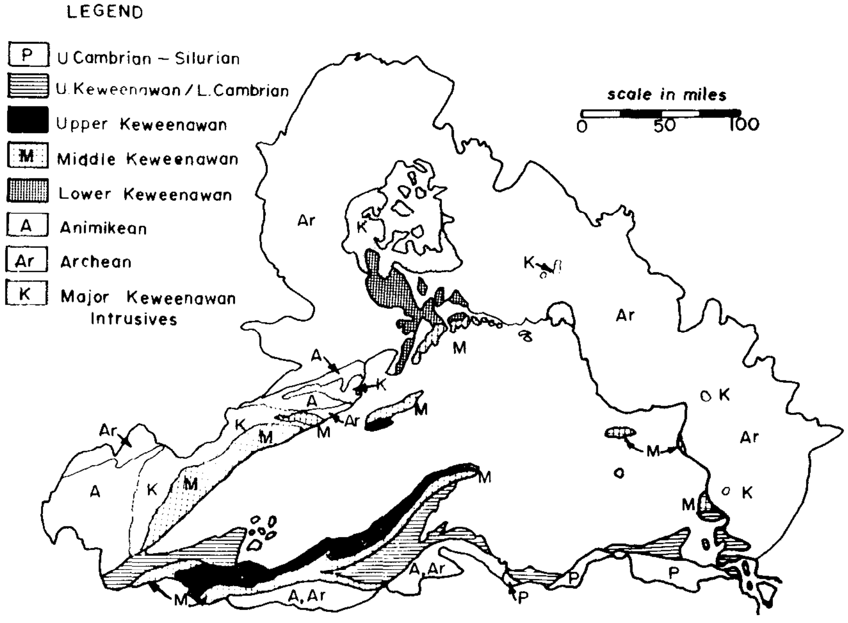

Fig. 3. The general geology of the Lake Superior drainage basin modified from Halls and West, 197 1).

east, the north and the northwest (Fig. 3). The area is characterized by irregular tumbled hills which are, in fact, the roots of ancient mountains. Their peaks rarely reach 610 m (2000 ft) above sea level and the local relief is also generally moderate, varying between 61 and 152 m (200 and 500 ft). Because the uplands rise abruptly from the lake many watersheds are short and near torrential. However, numerous fault valleys provide access to the interior of the drainage basin and carry major rivers.

The dominant rocks are batholithic granites of Archean age (Fig. 3), which potassium-argon radioisotope dates place at between 2300 and 2600 million years of age. At widely scattered locations in this sea of granite extensive, irregularly shaped areas of volcanic rocks or metamorphosed sediments, or both, mark the remnants of a cover which was folded, sheared and metamorphosed by an Archean orogeny (Pye, 1969).

The granitic rocks are of rather variable composition, quartz and feldspar porphyries, quartz diorites, syenite, granodiorite and pegmatites occur with the granite. The volcanics are predominately basic lavas though rhyolites also occur. The common metasediments are slates, greywackes and conglomerates with subordinate quartzites and limy carbonate rocks. Iron formations, usually of interbedded chert and magnetite-hematite or siderite are fairly common. Many of the sediments and volcanics have been highly metamorphosed and/or granitized to form granitic gneisses, and are often intruded by sills and dykes of gabbro and diorite. Ore bodies of copper and zinc are of widespread occurrence in the metamorphosed volcanics and sediments. Occurrences of other elements, such as beryllium, molybdenum and lithium may be associated with pegmatites or quartz near the boundaries of granitic batholiths.

The Southern Province of the Shield invests both the north and south shores of the western half of the lake except where the Bayfield-Jacobsville formation is apparent along the shoreline. These rocks extend far to the south and west of the Lake Superior drainage basin. The topography is hilly, usually of somewhat lesser elevation than in the Superior Province but characterized by steep sided ridges and buttes with local relief as great as 213 m (700 ft). With the exception of minor outcrops of Archean rocks in the south-central part of the drainage basin, the formations of this Province are of Proterozoic age and are divided into two units, an older Animikie and the Keweenawan. The Animikie formations consist of little altered conglomerates, interbedded shale and volcanic tuffs, interbedded cherts and taconites, and cherts and carbonates which may be dolomitic or ferruginous. Algal cherts appear locally. The oldest of these beds have K-Ar ages in the 1650 to 1800 million year range. The various beds have been extensively eroded since their deposition, and in consequence only remnants are now exposed. They are most prominent on the north shore near Thunder Bay (Fig. 3). Buried Animikie sediments are unconformably overlain by lower Keweenawan formations. The oldest of these are also sediments but have little surface exposure-around the margin of the lake. Along the north shore, near the apex of the lake, where they can be found, they consist of conglomerates, prominent white quartz sandstones, reddish shale, dolomites and dolomitic limestones which owe their colour to the presence of hematite.. Middle Keweenawan formations consist of massive flows of basic lavas with interbeds of conglomerates and sandstones. Copper deposits are prevalent in these formations wherever they occur. These lavas are conspicuous at many points around the shore of the lake, not only about its western half but also in isolated exposures along the southeastern shoreline (Fig. 3). The lava sequences are thick, as much as 9144 m (30,000 ft) in some places (Halls and West, 1971) and almost without exception they dip inward from the shore under the lake (Pye, 1969). Associated with the middle Keweenawan flows of lava were frequent intrusions in the form of massive sills and dykes of diabase, which may be found in one form or another throughout the entire watershed. In the western part of the basin fine grained shales and sandstones of the upper Keweenawan sequence overlie the lavas, and are themselves disconformably overlain by the Bayfield-Jacobsville formations.

The entire Lake Superior drainage was glaciated during late Wisconsin time, and did not emerge from the ice until the retreat of the Laurentide ice front between 13,000 and 9,000 years B.P. (Prest, 1970). During that interval a number of pro-glacial lakes occupied or overflowed the Superior basin, draining first to the Mississippi and later to the lower lakes, while themselves receiving, at one time or another, the discharges from two transitory ice margin lakes of equal or larger size, Lake Agassiz to the northwest and Lake Ojibway-Barlow to the northeast, as well as a series of lesser lakes between them in the northern part of what is now the Lake Superior drainage (Fig. 4). As might be expected, the surficial deposits overlying the bedrock are largely composed of glacial tills, or sediments deposited in melt-water streams and in the pro-glacial lakes and their associated drainage streams.

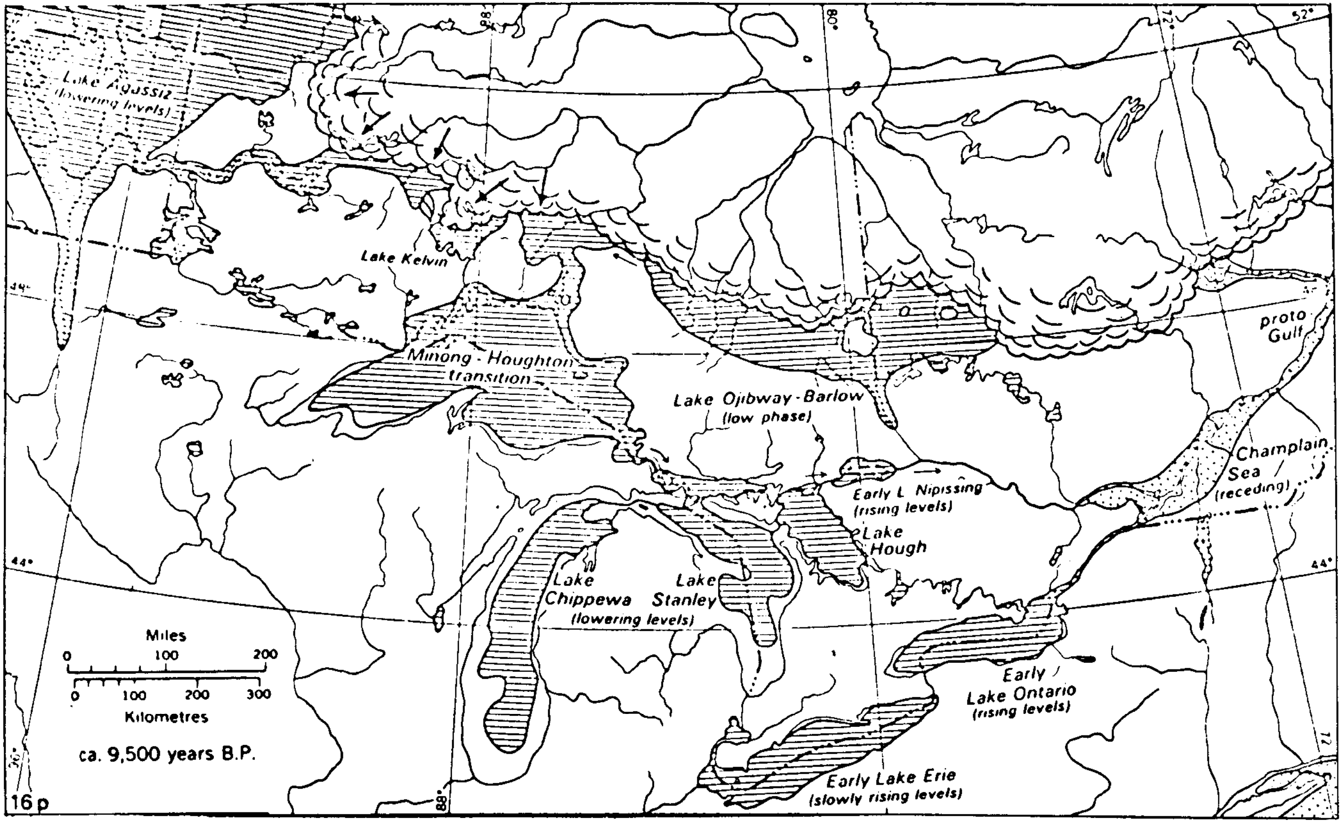

Fig. 4. Glacial lake phases about 9,500 B.P. illustrating interconnections with adjacent proglacial lakes (from Prest, 1970).

It is generally conceded that the tills are derived from, and share the lithology of, the local bedrock except where lacustrine sediments have been reworked by a local readvance of the waning ice sheet. Thus in areas underlain by crystalline Archean and Proterozoic igneous rocks or metasediments the tills are stony sands often with a strong admixture of boulders and bearing little silt or clay. Tills derived from the less altered Proterozoic sediments are generally less stony, have a higher proportion of silt and often show a high carbonate content. Clay tills are common in the northeastern part of the drainage, in and near the areas once occupied by pro-glacial lakes.

A number of authors (Dell, 1963; Boissonneau, 1966, 1968; Zoltai, 1965, 1967) have drawn attention to the transport of Palaeozoic rock fragments from the Hudson Bay lowlands southeasterly into the northeastern part of the Lake Superior drainage. These rocks are primarily siltstones, limestones or dolomites, often fossiliferous, whose admixture with the local tills renders them quite limy, as much as 40% carbonate-in the northern part of the drainage and lesser amounts southward. Southeast of the lake, tills derived from Palaeozoic strata are also strongly calcareous. Deposits of stratified sand and gravel occur throughout the area as interlobate moraines, outwash plains and eskers. Glaciolacustrine deposits of stone-free sands, silts, clays and varved clays cover extensive areas in the northern part of the drainage and are, as would be expected from their location, often limy.

The depth of these deposits varies according to the bedrock topography and the nature of their origin. Thus the principal accumulations resulting from direct glacial action, moraines, eskers and outwash plains, may contain as much as 60 m (200 ft) of till. Beds of lacustrine sediments may reach depths of 12 m (40 ft) as may till deposits in valleys, while the ground moraine on the uplands ranges in depth from nil to approximately 3 m (10 ft) (Zoltai, 1963, 1965, 1967; Boissonneau, 1966, 1968). Generally drift depths are shallower to the east and north.

It is questionable whether a meaningful statement of the average chemical composition of the rock in the land drainage basin can be derived. Quite apart from any problems of technique in the performance of the analyses it is obvious that collection of a genuinely representative series of samples and the derivation of appropriately weighted mean values for the parameters of interest present major problems in sampling design. Moreover, the diversity in both parent materials and depositional mechanism imply a high degree of variability with a consequent need for a large number of samples to provide estimates of useful precision. A lucid discussion of these problems has been provided by Shaw et al. (1967), who undertook to estimate the chemical composition of the Canadian Shield. Among the suites of samples analyzed were 8,076 rock powders collected from Superior Province of the Shield. Unfortunately none of these were drawn from within the boundaries of the Lake Superior drainage basin, having been taken from an area well to the north and slightly to the west of it in the Red Lake-Lansdowne House area, so that they may be less than fully representative of the bedrock and till from that part of the Lake Superior drainage which lies in this Province. Nonetheless, because both areas have a comparable history of glaciation and inundation by pro-glacial lakes and both stand in similar proximity to the Hudson Bay lowlands, Table 3 presents these

Table 3. The average chemical composition of rocks from Superior Province of the Canadian Shield. Adapted from Shaw et al. (1967) (Wt %)

0	41.19	Mn	0.07
Si	30.99	S	0.03
Al	8.13	F	0.03
Fe	3.10	Cl	0.01
Ca	2.84	V	0.0068
Na	2.87	Zr	0.0058
K	1.87	Cr	0.0054
Mg	1.24	Ni	0.0022
Ti	0.28	CU	0.0017
Ba	0.06	co	0.0012
P	0.06	Be	0.00011
Sr	0.05		

estimates as the best currently available. There are no comparable estimates for the remainder of the drainage basin although the geological literature abounds in accounts of the heavy metal suites and mineralogical composition of the rock formations in various parts of the drainage basin which are of economic or other interest (see, for example, Dreimanis et al., 19.57; Hamblin, 1958; Dell, 1963; Stockwell et al., 1971 and their lists of references).

Climate, soils, and land use

The mean annual air temperature of the Lake Superior basin is quite low, virtually 2 C (35-36 F) (Thomas, 1953). Only the period from June 1st to September 15th is completely free of frost and even for hardy species of plants the growing season scarcely exceeds 160 days (Atlas of Canada, 1957). Mean annual precipitation amounts to approximately 816 mm (32 in) of which between 20 to 40% falls as snow depending upon location. Fig. 5, taken directly from Hills (1959), shows in a general way the isopleths of both mean daily July temperature and mean annual total precipitation, illustrating the north-south gradient in temperature and the east-west gradient in precipitation.

Under these climatic conditions a variety of soils are developed depending on drainage and mineral substrate. Poor drainage leads to the development of peat deposits and peat-gleis. In the northern part of the watershed the frequent occurrence of level, slowly permeable, lacustrine clays has led to the accumulation of two feet or more of peat over extensive areas. In the southern part of the drainage where such conditions are less frequently encountered peat deposits are less widespread. On well drained sites, more or less well developed Podzolic soils have developed over acid parent materials throughout the northern part of the drainage while Luvisolic soils have developed where the parent materials are neutral or alkaline and the climate a little milder. Regosolic mineral soils with little organic content are common in the granitic areas with thin tills (Hills, 1959; Canada Dept. Agr., 1970).

The drainage basin is still almost entirely forested with scattered areas cleared of trees and given over to general agriculture (Fig. 6). North of the lake lie extensive tracts of boreal spruce-fir forests of which the characteristic species are balsam fir *(Abies balsamea* (L.) Mill.), black spruce *(Picea mariana* (Mill.) B.S.P.) and white spruce (P. *glauca* (Moench) Voss) with groves and

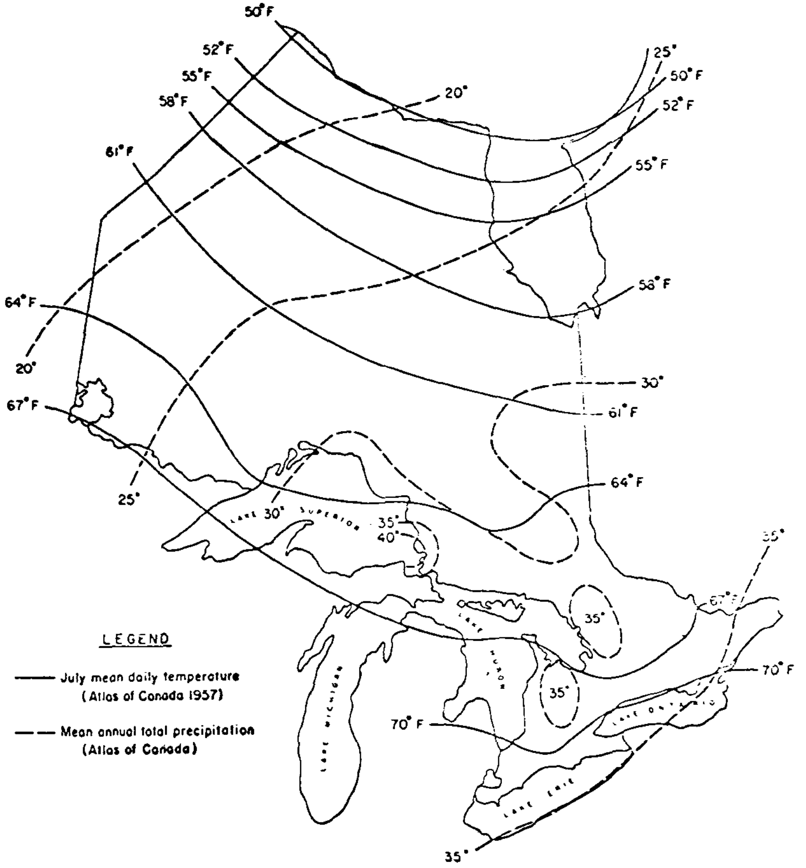

Fig. 5. Significant trends in the distribution of atmospheric temperature and moisture (from Hills, 1959).

thickets of such deciduous species as trembling aspen *(Populus tremuloides* Michx.), white birch *(Betula papyrifera* Marsh.), and alders *(Alnus* sps.). These forests have long been cut to provide pulpwood for paper making which has been the primary industry in the area. Until the last- decade pulp logs were commonly brought down from the forest by floating them downstream on the spring floods, accumulating them in sheltered bays on the coast and towing them along the lake in large rafts to the mill. This practice can hardly have failed to affect the streams concerned not only because of the mechanical scouring by the logs themselves but because water levels were commonly controlled by one or more dams and the stream bed itself altered to clear away obstacles. In bays where the pulp logs were stored and in the narrower channels through which they were rafted there are often deep beds of bark and waterlogged wood marking many years of accumulation of allochthonous materials in Lake Superior itself. This is now largely a thing of the past and the great bulk of the pulp moving to the mills is carried by

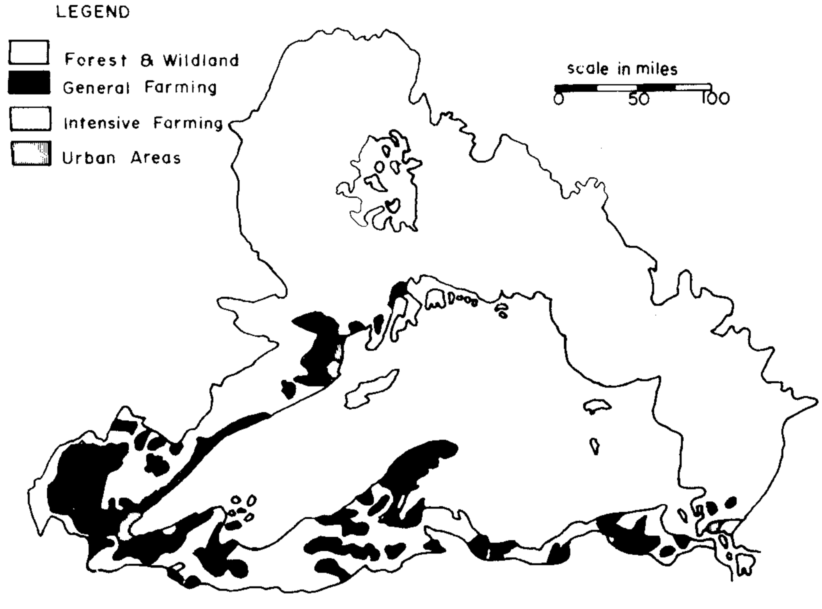

Fig. 6. Land use in the Lake Superior drainage basin (after Lee and Beaulieu, 1971).

specialized trucks. The mills, themselves, however, remain at the water's side where their waste effluents have contributed a substantial part of the industrial pollution currently affecting local areas of the lake.

South of the lake, the forest cover is deciduous and dominated by hard maple *(Acer saccharum* Marsh.) and yellow birch *(Betula lutea* Michx.). White and red pine *(Pinus strobus* L. and *Pinus resinosa* Ait.) as well as white birch, balsam and black and white spruces occur as secondary species. This forest is regularly cut for large logs of yellow birch and maple which are utilized in making veneers and other hardwood products. These are, however, taken from forest to mill by truck or by rail so that logging operations do not directly affect the watershed streams or the lake itself. Moreover, since the sawmills are usually well removed from the shore, their operations result in little, if any, contribution of waste products to the lake.

Between the boreal and the southern deciduous forests is an intermediate area, dominated by the white and red pines but with extensive elements from the adjacent forest types (Hills, 1959). Such cutting as is now practised there is largely directed at these elements rather than at the pines themselves. However, the pines were formerly dominant throughout the present hardwood areas and formed the basis of the original lumbering developments in the drainage basin, especially along the U.S. shore. There lumbering began about 1850 and as production outstripped local demand, became a major industry exporting its lumber to the markets of the mid-western U.S. initially by ship and eventually by rail. As long as they lasted, white and red pine were selectively cut and the volume of timber taken from the area was staggering. A single company shipped, in 1870, 75 million feet of lumber and 30 million shingles. Twenty-five years later the annual production from two counties alone was 154 million feet of pine lumber plus 6 million shingles. The exploitation was ruthless and complete. By 1896 pine was becoming scarce along most of the south shore and production records begin to indicate that hemlock (Tsuga canadensis (L.) Carr.), spruce, maple (presumably hard maple), red oak (Quercus *rubra* L.) and white and yellow birch were being cut. With the depletion of the timber reserves of the south shore the attack was shifted to the less productive U.S. north shore, which between 1890 and 1924 was progressively stripped of its pine forests, the last big shipment of pine occurring in the latter year (Nute, 1944).

In the rapacious exploitation of these forests there was no element of sound forest management or of general conservation. Clear cutting was the rule, tops and limbs were left where they had been cut, and fire was a common sequel, so that the understory was often destroyed, the forest litter burned away and the exposed soils leached and eroded. As with the pulp log industry along the Canadian north shore, the timber was taken to the sawmills by "driving" the rivers so that extensive scouring of stream beds and introductions of allochthonous materials must have occurred. Moreover, as in the pulp log industry the sawmills were located at the shore, often on the estuaries of major rivers down which the logs were brought, and their operations resulted in the introduction of large quantities of sawdust and coarser woody materials to neighbouring areas of the lake (Milner, 1874; Nute, 1944). Considering the experience at Hubbard Brook following deforestation of part of that watershed (Borman and Likens, 1970) it is difficult to believe that this devastation of the climax forest ecosystem did not also greatly alter the composition and quantities of dissolved materials reaching Lake Superior.

Although it is not apparent on Fig. 6 (because of the small areas actually involved) mining has been as important as lumbering and more enduring. Thus extensive iron mining is still practiced in the drainage, characteristically in the earlier Proterozoic deposits along the southwest and northwest shores. Somewhat similar iron formations of Archean age are mined along the east shore. Zinc and copper ores and native copper have also been intermittently mined in these same general areas, Most of the mines have been located some distance from the Lake Superior shore but where water supply has been critical processing plants have often been located at the waters edge well removed from the mine. The waste discharges from such plants constitute a significant part of the industrial pollution now affecting local areas of the lake.

Chemistry of influent streams

Apparently, interest in the manner in which nutrients are conveyed from Lake Superior's large and complex watershed to the lake has only recently begun to develop. There appear to have been no studies relating the chemistry of the drainage basin's interstitial waters to that of the rain falling on it, the soil itself or the water of the drainage streams. However, because the biological activity of the selective toxicant TFM (3-trifluormethyl-4-nitrophenol), used to destroy larval sea lamprey in their natal streams, is influenced by the physical and chemical properties of the stream water, the U.S. Bureau of Commercial Fisheries examined the water quality of 99 tributaries to Lake Superior during the period 1962-1965 (Zimmerman, 1968). Three of the streams were sampled at regular intervals through the season at several stations. The remaining 96 were sampled as opportunity offered. More recently, streams tributary to the extreme western extremity of the south shore have been rather intensively sampled over a period of several summer months to establish the character of what has been called by the authors a "wild river" (Bahnick, Horton, and Roubal, 1969, 1970). An eighteen month study of two small tributaries to the southern part of the eastern shore has just been completed (Dr. W. Kwain, personal communication).

All these studies, not unexpectedly, indicate that the parameters measured vary with flow. High water, resulting from heavy rains or melting snow, increased turbidity, colour and the concentrations of tannin and lignin-like materials but diluted most of the inorganic ions. Conversely, low flows during the heat of summer and again under winter ice had exactly the opposite effect. Detailed comparison of the data obtained in the four studies is rendered difficult not only because the authors elected to measure different things but also because they employed different analytical methods. Nonetheless, Table 4 has been constructed to provide some idea of the characteristics of these streams.

On the whole they appear remarkably similar although examination of the original accounts will show that there are minor but significant differences not only between streams but between the individual tributaries making up a particular drainage. For the two rivers which they have described, Bahnick et al. (1970) ascribe these differences to differences in the size and nature of the two drainage basins. It is also apparent from examination of Zimmerman's (1968) data that the water chemistry reflects the geology of the basin. Thus, his streams 18, 19, 23, and 24 drain into the lake from watersheds largely underlain by middle Silurian dolomitic limestones and show concentrations of Ca^{++} ranging from 17 to 34 ppm, Mg^{++} concentrations extending from 6 to 16 ppm, and total alkalinities from 52 to 140 ppm, $CaCo_3$, all much above values from hardrock areas.

There is no comparable information for north shore streams.

Seiches and currents

The dispersal of both the dissolved and particulate matter brought to the lake by its tributaries is effected by water currents in the lake. Lake Superior, like the other Great Lakes, is subject to internal seiches with consequent fluctuating levels and corresponding currents. Ragotzkie, Ahrnsbrak and Synowiec (1969) have described the role of horizontal currents associated with seiche generated oscillations of the surface of Chequamegon Bay, Lake Superior. The seiche activity showed periods of 12, 21, 36, 62, and 140 minutes, the latter seiche having a nodal line near the mouth of the bay so that the horizontal currents across this line served to flush water into and out of the bay. Assuming the surface of the bay to remain a plane, Ragotzkie et al. (1969) calculate that a 10 cm vertical oscillation could result in an exchange rate of 5% of the volume of the bay (1.4×10^9 m^3) per day.

Table 4. Estimates of some parameters of the water chemistry of streams tributary to the south shore of Lake Superior.

	Southwestern Rivers		South-central Rivers[c]			Southeastern Rivers[d]	
Measurement	Brule[a]	Poplar[b]	Big Garlic	Little Garlic	Chocolay	Stokely	Carp
pH	7.7±0.6	7.7	7.0-7.9	7.1-8.0	7.2-8.3	6.8-8.4	6.8-8.1
Total Alkalinity (ppm CaCo3)			14-62	18-78	22-82	18-41	1.5-33
Conductivity (micromhos/cm^3)	106±13	134	40-124	48-146	66-156	40-191	67-146
Ca++ (ppm)			6-20	8-26	9-26		
Mg^{++} (ppm)			1.5-5.8	1.5-5.3	2.9-7.8		
Nitrate (ppm)	0.41±0.24	0.38	0.1-2.9	0.1-2.2	0.3-3.9	O-1.0	0-1.0
Orthophosphate (ppm)	0.020-0.080	0.020-0.110					
Polyphosphate (ppm)	0.000-0.175	0.017-0.240					
Dissolved O_2 (% sat)	56-100	50-100				77-100	77-100

a,b Bahnick et al. (1969, 1970)

c Zimmerman (1968).

d Kwain (personal communication).

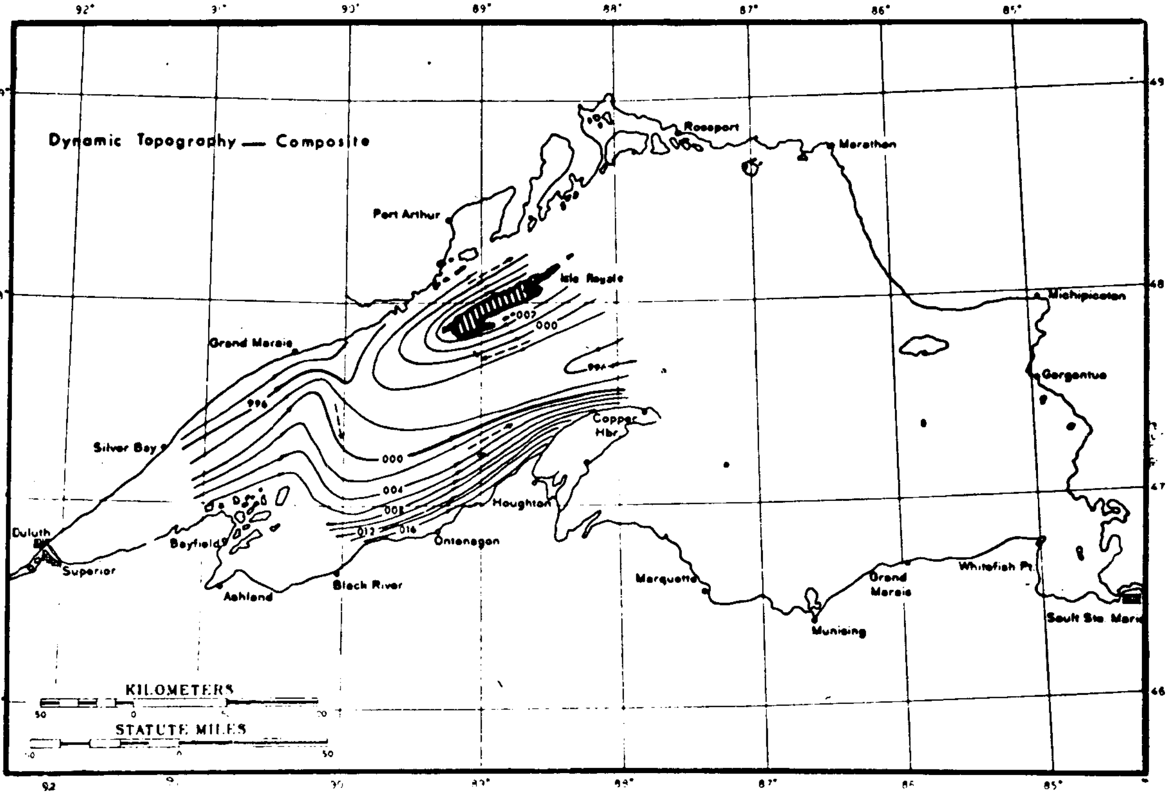

Fig. 7. Summer circulation patterns of western Lake Superior (from Adams, 1970).

Also serving to flush Chequamegon Bay are directly wind-driven currents which either move the warmed epilimnion water out from the bay to the open lake, with a consequent deeper counter current, or conversely bring open lake epilimnion waters in with a consequent outflow from the hypolimnion of the bay, depending on wind direction. Because of the rather regular passage of cyclonic weather systems during the summer, reversals occur with a period of between five and ten days so that the entire bay flushes about every two weeks. Ragotzkie et al. (1969) draw attention to the analogy between this process and that of the tidally-driven oscillations of an estuary.

It has long been known from drift-bottle studies that the general pattern of the surface circulation of Lake Superior water is counterclockwise (Harrington, 1894; Beeton, Johnson and Smith, 1959). Studies in the past decade are beginning to give more precise understandings of current patterns in some parts of the lake. In the western half of the basin the predominantly westerly winds of summer combine with surface warming to generate an easterly drift along the south shore and upwelling along the north shore (Adams, 1970). Fig. 7, based on his dynamic height calculations, shows a typical summer current pattern (actually a composite of his observations). Conspicuous features of this circulation are the clockwise circulation about Isle Royale with velocities of 15 cm/s north of it, the counterclockwise circulation in mid-lake, which represents the westward end of a large area of cold, upwelling water, and the strong geostrophic current sweeping past the Keweenaw Peninsula on the south shore. The last has been closely examined by Ragotzkie (1966) and Smith and Ragotzkie (1970) who have shown the measured currents to often be greater than 30 cm/s in some part of the cross-section of the current, and significant speeds to extend down to a depth of 60 m. They warn that the dynamic height method significantly underestimates the velocity of this current. Adams (1970) also notes that two or three days of easterly winds disrupts this pattern and results in the development of a counterclockwise circulation in the western arm with cessation of the upwelling along the north shore. Similar studies of the circulation in eastern Lake Superior have yet to be undertaken, ‘but the existence of a persistent and extensive area of upwelling with temperatures of 5 to 6 C in high summer has been demonstrated by the use of infrared radiation patterns by Ragotzkie and Bratnick (1965) who postulate the development of a persistent cyclonic gyre as a result of a prevailing wind stress. Little is known of circulation patterns at other seasons, particularly in the winter, but Murty and Rao (1970) have employed a steady state linear model of wind-driven circulation, under a number of simplifying assumptions appropriate to the isothermal conditions obtaining spring and fall, to simulate them. Fig. 8 displays the patterns generated by the application of their model under two different circumstances, the first assuming a nondivergent wind field, the second a divergent wind field, both with variable stress in the x and y directions. These have not been compared to observed data, but nonetheless are of interest as examples of the complex circulations which might, not unreasonably, be expected at these seasons.

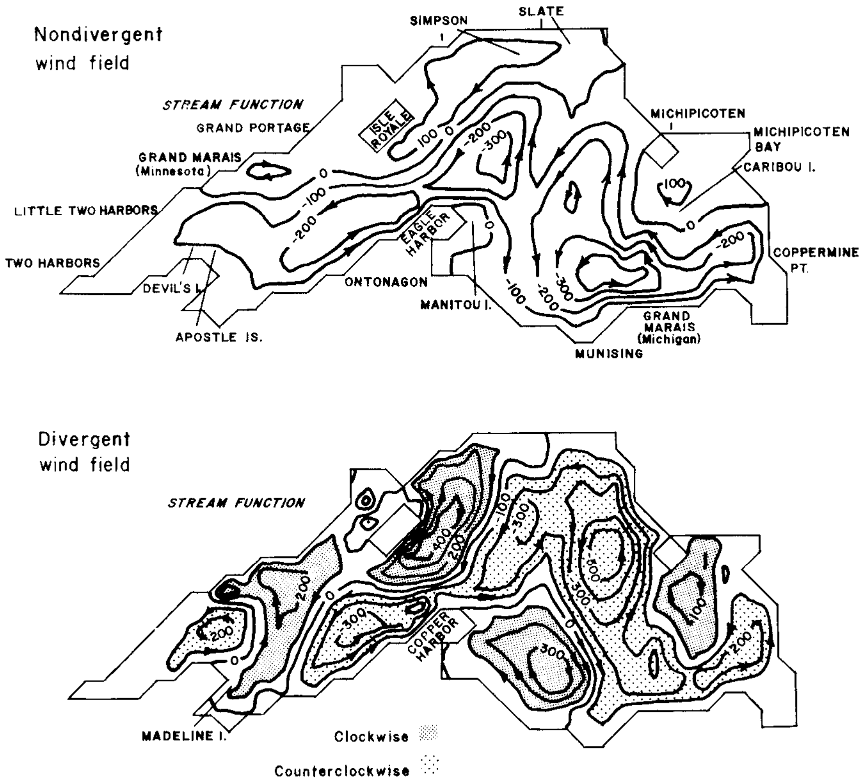

Fig. 8. Hypothetical spring-fall circulation patterns of Lake Superior (from Murty and Rao, 1970).

Temperature regime

In inshore waters, particularly those sheltered by islands, persistent thermal stratification is evident by mid-July, when the epilimnion may reach a depth of 18 m (10 fath). In more exposed waters, however, with their wind stressed circulations and large pools of upwelling hypolimnetic waters, stratification is often well developed during periods of prolonged light winds or calm only to be disrupted by a few days of persistent wind from the same quarter. The transient nature of the stratification is, for obvious reasons, more evident in the northern half of the lake, and results in surges of very cold water up the channels leading to the sheltered bays of the north shore during periods of upwelling.

Ice cover

Lake Superior does not entirely freeze over during the winter, the general pattern of the growth and decay of the ice cover having been summarized by Marshall (1967) from whom Fig. 9 is taken. Because of the persistent open water, deep mixing is characteristic of winter conditions in the lake and can lead to the development of homothermous water of about 2 C to

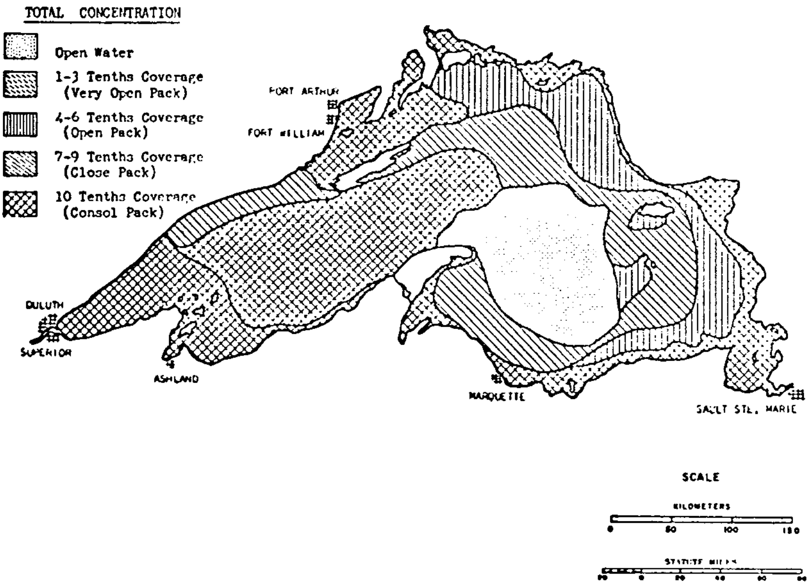

Fig. 9. Maximum extent of Lake Superior ice cover, mid February to mid March (from Marshall, 1967).

a depth of 183 m (100 fath) (Beeton et al., 1959). Winter stratification does, however, occur, the deeper waters remaining at the temperature of maximum density, as they do throughout the year.

Projected thermal loads

Denison and Elder (1970), reviewing the growth of man-made thermal inputs to the Great Lakes and projecting them to the year 2000, have suggested that a ten-fold increase in the present thermal input to Lake Superior can be expected by that date. However, the anticipated thermal load of 0.0005 kilocalories/hr/m^2 (0.022 BTU/hr/ft^2) is scarcely a fifth of the load now borne by Lake Ontario or Lake Erie so that, disregarding possible local problems, we may reasonably consider it unlikely that any measurable effect will be felt.

Light penetration

In 1665 the clarity of Lake Superior water so impressed the Jesuit missionary Father Claude Allouez that he remarked that objects at the bottom could be seen to the depth of six “brasses.” Since there are 1.13 brasses to the fathom this amounts to a transparency of virtually 10 m (32 ft) which compares quite favourably with modern observations which record summer Secchi disc readings ranging from 1 to 23 m (3 to 75 ft) in situations ranging from turbid harbours to the open lake (Eddy, 1943; Ruschmeyer, Olson and

Bosch, 1957; Callender, 1969). Beeton (1962) noted that the spectral distribution of light at depth is in the blue-green range in Lake Superior and lists the extinction coefficients shown in Table 5. These values were obtained in the island area of southwestern Lake Superior and Beeton warns that they may not be representative of the open lake which he suggests is probably very similar to Lake Huron. Values for that lake are also included in Table 5.

Sediment and water chemistry

Farrand (1969) indicates that the bottom of the lake is deeply covered with glacial drift and sediments, up to 30 m (100 ft) in the eastern basin and commonly better than 60 m (200 ft) in the western basin where as much as 300 m (1,000 ft) occurs in the deep trench along the northwest shore. Deep cores show a complex of glacial deposits lying on the bedrock floor followed by long sequences of late glacial and postglacial clays (Reid, 1961; Callender, 1969). Callender (1969) has considered the geochemical characteristics of these sediments on the basis of samples largely taken in the eastern basin. His results indicate that they have been deposited in a pelagic environment and show no evidence of accelerated erosion in the drainage basin. The chemical composition of both the sediments and the interstitial water squeezed from them is presented in Table 6 and compared with that of the lake water. The

Table 5. Vertical extinction coefficients in Lake Superior water for light in five wave bands. Lake Huron values in brackets. From Beeton (1962).

Wave band (mμ)	Extinction Coefficient
300-420	0.41 (0.28)
410-440	0.27
440-490	0.22 (0.10)
490-540	0.20 (0.11)
610-750	0.39 (0.48)

Table 6. The average chemical composition of Lake Superior sediments (weight percent), their interstitial waters (ppm), and lake water (ppm) from Callender (1969).

Component	Sediment	Interstitial Water	Lake Water
Calcium	1.38	28.4	12
Magnesium	1.08	4.3	2.8
Iron	2.36	3.48	0.011
Manganese	0.067	1.37	0.002
Sodium		3.3	1.1
Potassium		1.4	0.6
Chloride		3.7	1.9
Silica	-	34.1	2.1
Carbonate	1.14	-	-
Organic Carbon	2.44		
Total Nitrogen	0.23	-	-
pH		6.99	7.4
Ca/Mg	1.3	6.61	4.28
Fe/Mn	35	2.54	5.50

interstitial water is in equilibrium with kaolinite and approaches saturation with respect to montmorillonite, chlorite, amorphous silica, and calcite but is undersaturated with respect to dolomite. Although the organic carbon content is relatively high there is no indication of recent enrichment at the surface of the sediments. Gumerman (1970) has demonstrated the capacity of sterilized sediment derived from western Lake Superior to take up and release phosphate in aqueous solution.

Lake Superior is generally regarded as being in a pristine state not far removed from the composition of rain water. In fact, Kramer (1964), notes that the ionic composition corresponds closely to a mixture of runoff in equilibrium with sialic rocks and their weathering products, kaolinite-illites, and rainfall with a composition akin to distilled water. Weiler and Chawla (1969), in addition to presenting original data on the major and trace elements encountered during systematic monitoring of all the Great Lakes during the period July to November, have provided a useful review of the earlier work of Beeton (1965) and Kramer (1964). As in most such studies to date, interest has centered upon comparisons between the lakes and on changes in composition with time. Table 7, adapted from Weiler and Chawla (1969), lists the chemical characteristics of Lake Superior water from these and other sources. Interestingly, in discussing the minor element concentrations, Weiler and Chawla (1969) note that high concentrations of Fe, Cu, Zn, Ni, occur in the western end of Lake Superior and around Nipigon Bay on the north shore, a circumstance which they suggest is related to mining activities in these regions.

Figures 10, 11 and 12, taken directly from Weiler and Chawla (1969), show the changes with time in the chemical composition and total dissolved solids of all five of the Great Lakes. For Lake Superior the general stability in water chemistry is quite evident and contrasts sharply with the conditions in the lower lakes. It has been generally considered that the slightly declining trend in total dissolved solids, sodium plus potassium, and perhaps chloride concentrations is not significant and that present conditions are primitive. Considering the history of timber exploitations in the drainage basin which, as

Table 7. The chemical characteristics of Lake Superior waters (after Kramer, 1964; Beeton, 1965; Weiler and Chawla, 1969; Winchester, 1970; Schelske and Callender, 1970).

Constituent	Concentration ppm	Constituent	Concentration ppb
Ca	12 - 13.2	P	5
Mg	2.7 - 2.8	I	1.1
Na	1.1 - 1.3	Zn	27
K	0.54 - 0.6	Cu	12
Si	3.2 - 3.9	Pb	2.2
SO_4	3.2 - 3.9	Fe	8
Cl	1.3 - 1.9	Ni	2
F	0.032 - 0.15	Cr	1
pH	7.2 - 7.8	Mn	< 1
SiO_2	1.87 - 2.01		
Alkalinity	46 - 52	Sr	32.5
HCO_3	51.3	NO_3-N	270
Total Dissolved Solids	52		

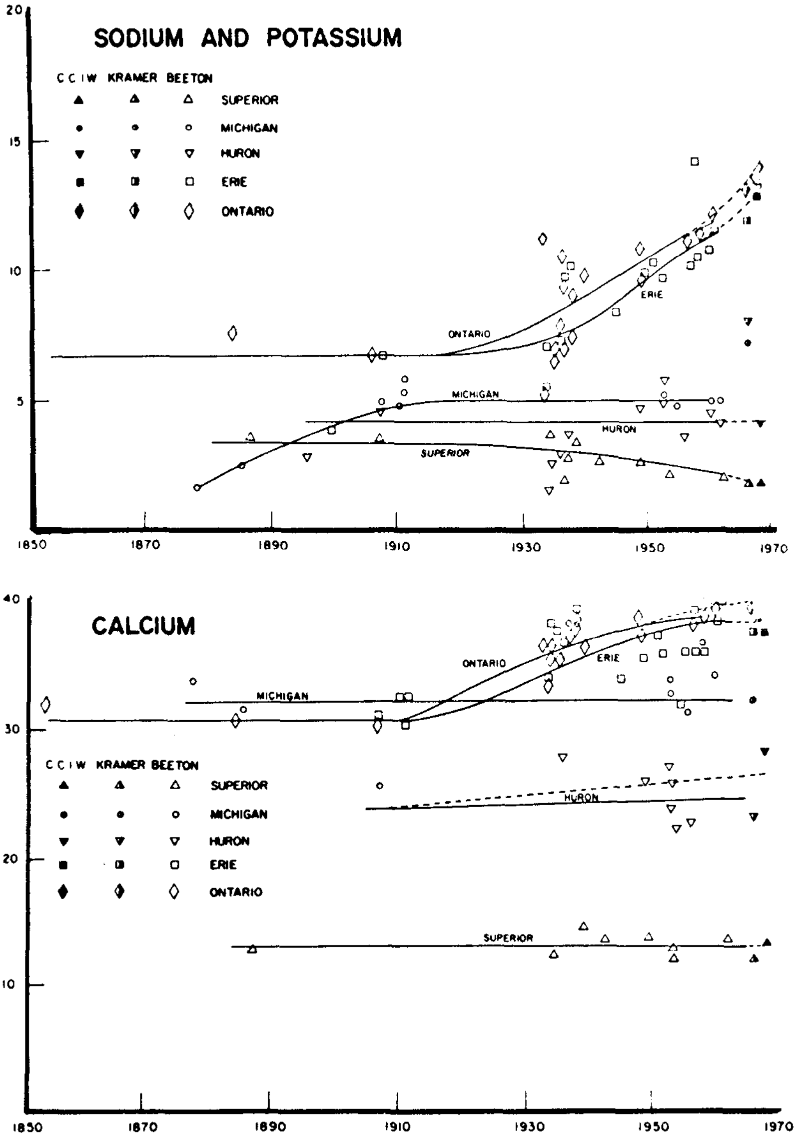

Fig. 10. Changes in concentrations of sodium, potassium and calcium in Great Lakes waters (from Weiler and Chawla, 1969).

earlier noted, must surely have dislocated the pattern of nutrient supply to the lake, these long term trends may in fact be real though very slow and reflect a return toward a pristine condition as a consequence of forest regeneration. **Considering the enormous volume of the Lake Superior basin** such a return would be expected to be slow.

On the assumption that the concentrations of all major ions are constant, Weiler and Chawla (1969) conclude that these concentrations are

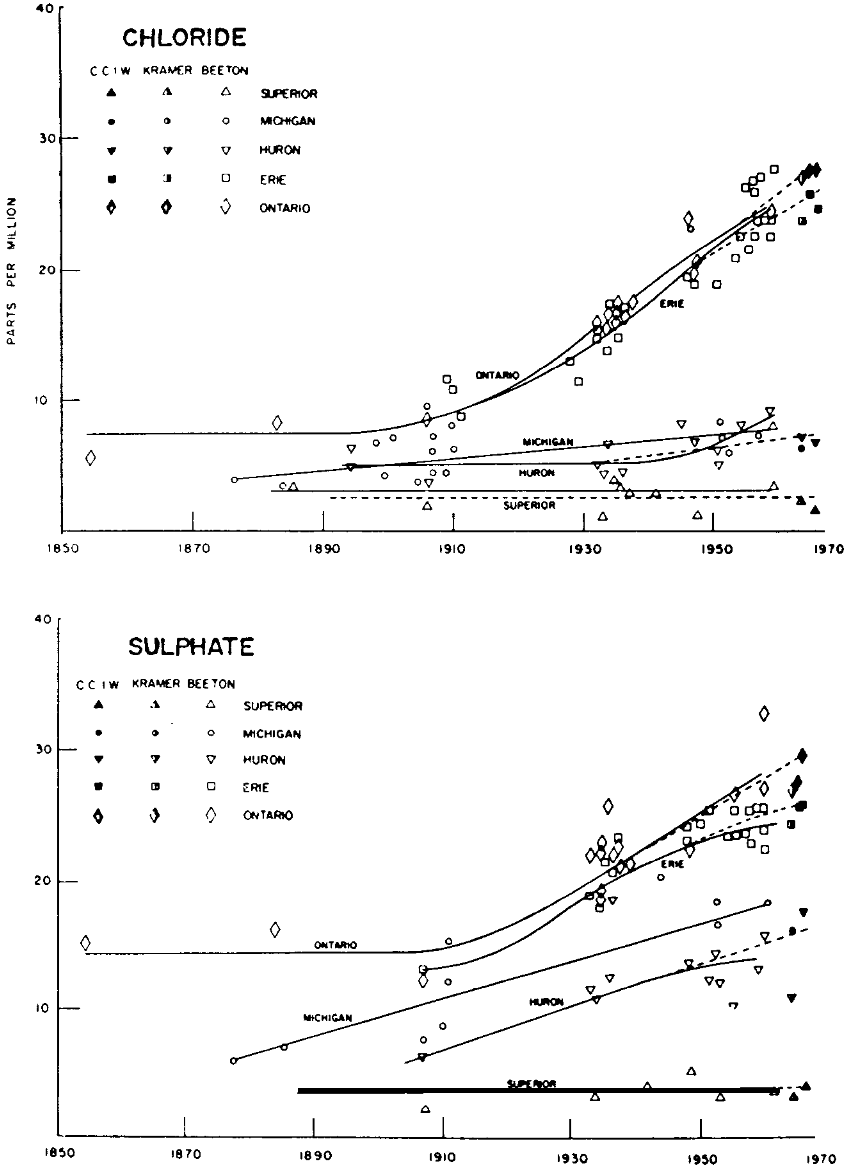

Fig. 11. Changes in concentrations of chloride and sulphate in Great Lakes waters (from Weiler and Chawla, 1969).

simply the result of a balance between the amount of dissolved substances added by runoff and that lost by outflow. They demonstrate that Lake Superior water is unsaturated with respect to both calcite and dolomite (see also Schelske and Callender, 1970) in confirmation of Kramer's (1964) contention that Lake Superior is unsaturated with respect to all constituents,

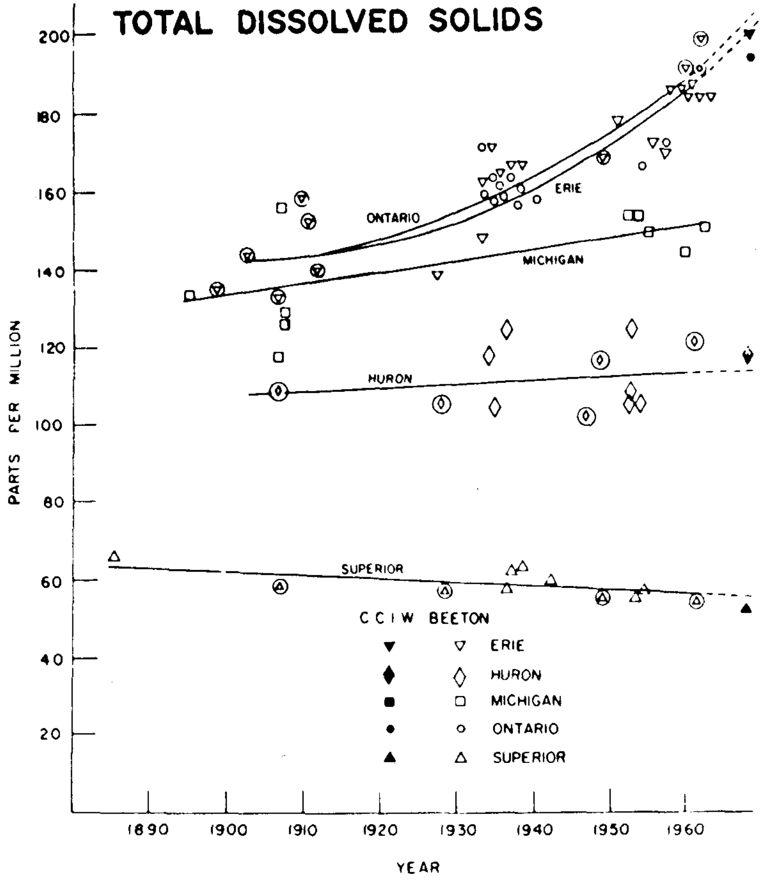

Fig. 12. Changes in concentrations of total dissolved solids in Great Lakes waters (from Weiler and Chawla, 1969).

being diluted by a factor determined by the ratio of rainfall on the lake to total rainfall in the drainage basin.

YEASTS AND MOLDS

In a brief, but interesting paper Hedrick, Cook, and Woollett (1968) reported on the occurrence of yeasts and molds isolated from samples drawn in the open waters of the west end of the lake, in areas near harbors and rivers, and in streams entering both the north and south shores of the lake. Although the authors do not suggest the use of either yeasts or molds as indicator species for the detection of pollution, they do point out a positive correlation between the organic nitrogen content of the sampled waters and the number of yeasts per litre of water sampled. Nitrate levels in the near shore waters of the lake were in the range of 0.30 to 0.45 ppm, while organic nitrogen values for the same stations ranged from 0.10 to 0.18 ppm. In contrast, the nitrate levels of streams ranged from 0.04 to 0.06 ppm, the organic nitrogen levels from 0.18 to 1.40 ppm. Yeast counts from the lake ranged from 5 to 55 organisms per litre and from the streams from 15 to 1000.

ALGAE AND PRIMARY PRODUCTIVITY

Periphyton

The epilithic periphyton of western Lake Superior have recently been investigated (Fox, Olson and Odlaug, 1967; Stokes, Olson and Odlaug, 1967) because it was expected that the production of this portion of the aquatic ecosystem might reflect the water quality at the location concerned. In depths to 35 ft, during the period July 19 to September 1, periphyton belonging to 33 genera, largely Bacillariophyceae, were identified as colonists on artificially denuded rocks in the study area. The average number of naturally occurring organisms in the range of depths concerned was approximately 500,000 per cm^2 of rock surface, corresponding to an average dry weight of 0.125 gm/cm^2. The concentrations of chlorophyll a, b, and c, as well as astacin and non-astacin carotenoids were shown to increase on a unit area basis with depth (Fig. 13) while the oxygen yield per mg of chlorophyll, 13.5 ml/hr at 2.5 ft, peaked to 22.3 ml/hr at 5 ft before falling off asymptotically through the remaining depths. Since the entire study area consisted of 321,226 m^2, the standing crop was estimated at 48.6 metric (53.6 U.S.) tons.

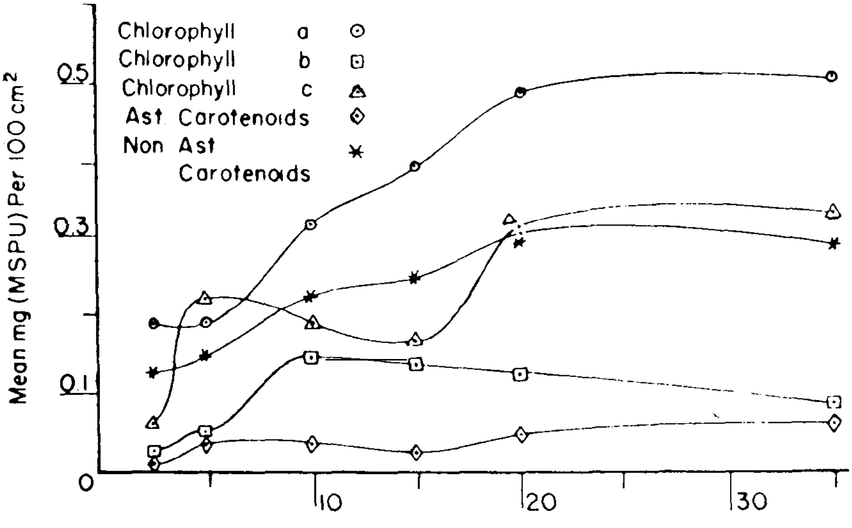

Fig. 13. Periphyton pigment concentrations per unit area at various depths (from Stokes, Olson and Odlaug, 1967).

Phytoplankton

The phytoplankton populations of Lake Superior are sparse and little studied. Basing her conclusions on collections from 14 stations scattered through the southern half of the lake, Holland (1965) demonstrated the existence of a diverse and widespread diatom assemblage. The principal diatoms in order of decreasing abundance were *Cyclotella glomerata-stelligera (= C. glomerata* and *C. stelligera* combined), *Cyclotella ocellata-kutzingiana, Fragilaria crotonensis, Rhizosolenia eriensis, Asterionella formosa, Synedra nana* and a species of *Stephanodiscus.* During the period between June and November, when the samples were taken, Holland (1965) found considerable variation from place to place in the species composition of the diatom flora and concentrations ranged from 68 per ml in offshore waters northwest of the Keweenaw Peninsula to 2,160 per ml in the island area of southwestern Lake Superior. Putnam and Olson (1966) following the phytoplankton assemblages at a single station along the northwest shore of the lake, found densities of less than 500 organisms per ml with a succession of forms being dominant at different times in the summer. The average standing stock in terms of cell number was made up of Bacillariophyceae (68%), Chrysophyceae (22%), Cyanophyceae (7%) and Chlorophyceae (3%). Beeton (1965) relies on earlier works by the same authors (Putnam and Olson, 1961) from the same general area to describe the predominant Lake Superior phytoplankton as *Asterionella formosa, Dinobryon, Syndera acus, Cyclotella, Tabellaria fenestrata,* and *Melosira granulata.*

Primary productivity

Schelske and Callender (1970) have drawn together the available information on primary productivity from these phytoplankton communities in Lake Superior, noting the differences between their own estimate of the rate of carbon fixation (4.7 mg C/m^3/12-hr day) and those of Putnam and Olson (1966) (4.5 to 13.4 mg C/m^3/day) and Parkos, Olson and Odlaug (1969) (17 mg C/m^3/12-hr day) which, in part, can be attributed to differences in methodology. They relate primary productivity to the concentrations of soluble nutrient elements, particularly nitrate, nitrogen and silicon, drawing attention to the fact that there are no material differences in the concentration of these nutrients between surface and near-bottom samples in Lake Superior, indicating that the sparse phytoplankton population was utilizing little of the available nutrient.

ZOOPLANKTON

A recent paper (Swain et al., 1970) provides a useful review of the limited literature describing Lake Superior zooplankton as well as discussing their vertical migrations. Eddy (1943) described the rotifers: *Keratella cochlearis* and *Kellicottia longispina;* the cladocerans: *Daphnia longispina* and *Bosmina longirostris;* the copepods: *Diaptomus minutus, D. sicilis, Epischura lacustris, Limnocalanus* macrurus and *Cyclops bicuspidatus* as common. Olson and Odlaug (1966) describe the density of planktonic Crustacea at a single station on the northwest shore of the lake as functions of depth, season, and time of day. Peak populations reached as high as 213,000 individuals per m^3 in August, the commonly taken crustaceans being *Limnocalanus macrurus, Bosmina coregoni, Daphnia pulex, Daphnia longispina, Polyphemus pediculus* and *Leptodora kindtii* in that order of abundance.

INVERTEBRATE MACROBENTHOS

Studies of the macrobenthos of Lake Superior have been limited, both in number and in geographic coverage. Thomas (1966) published lists of benthic organisms collected during the course of surveys of four north shore Lake Superior bays for larval lamprey. Hiltunen (1969) reports on the benthic fauna of extreme southwestern Lake Superior, particularly in the island region, and Alley and Powers (1970) report on the macrobenthos taken at 5 deep stations (97 to 335 m) in eastern Lake Superior. Adams and Kregear (1969), on the basis of samples drawn from 63 stations in the eastern basin of Lake Superior, have described three faunal environments: pelagic, boundary and shoal, characterized not only by their depth relations, as their names imply, but also by the composition and degree of sorting in the substrate. The boundary biotope is subdivided into a sand and a bedrock member. Fig. 14 illustrates the relative abundance of the more abundantly represented families of the macrobenthos in these biotopes. Hiltunen's samples appear to be intermediate between the pelagic and sand boundary biotopes, while those of Alley and Powers clearly were of the pelagic biotope. Alley and Powers have

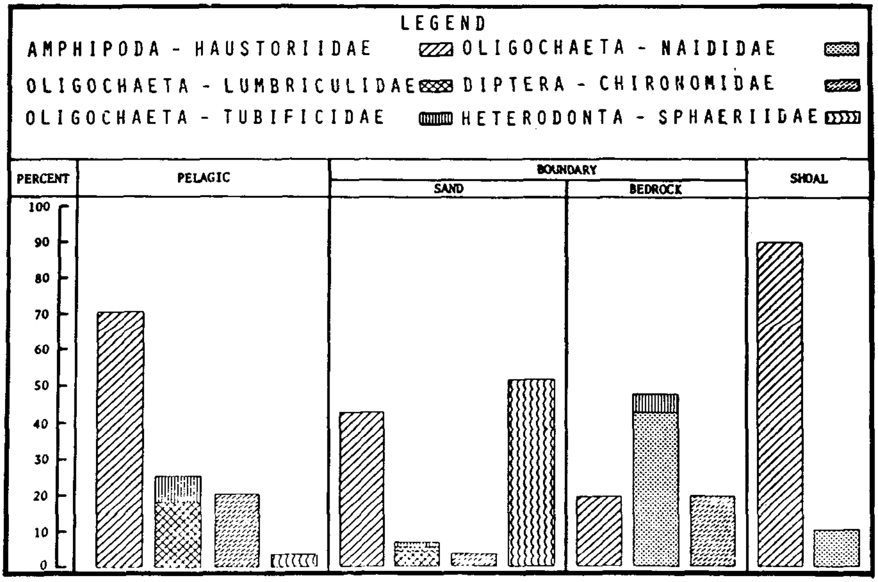

Fig. 14. Composition of the benthic fauna of eastern Lake Superior biotopes (from Adams and Kregear, 1969).

calculated the dry weight of macrobenthos to be 0.09 gm/m^2 for Lake Superior and express their conviction based on comparisons of the counts in their samples with those of Hiltunen that this figure probably reflects the overall distribution of benthic biomass. Its very low value is interpreted as indicative of extreme oligotrophy, as is indicated by Fig. 1.5 redrawn by Alley and Powers from Rawson (1953) and reproduced here.

THE FISHERIES

Presettlement fisheries

Narrative accounts of the exploration of Lake Superior in the 17th and 18th centuries note the existence of many Indian maintenance fisheries especially along the south shore (Ablon, 1671; Carver, 1778; Warren, 1957). Estimates of total yield from the lake are, of course, not available but local catches may have been substantial. The Jesuit Relation of 1669-1671 notes that ". . a single fisherman will catch in one night twenty large sturgeon, or a hundred and fifty whitefish, or eight hundred herring in one net." Elsewhere in the same source the fishery in the Ontonagon River was said to be ". . . carried on, day and night, from Spring until Autumn and it is there that the Savages go to lay in their provision."

During the latter part of this period a number of forts and trading posts were established about the lake for the purpose of trading, in furs, with the Indians. The largest of these, Fort William, was the capital of the Northwest

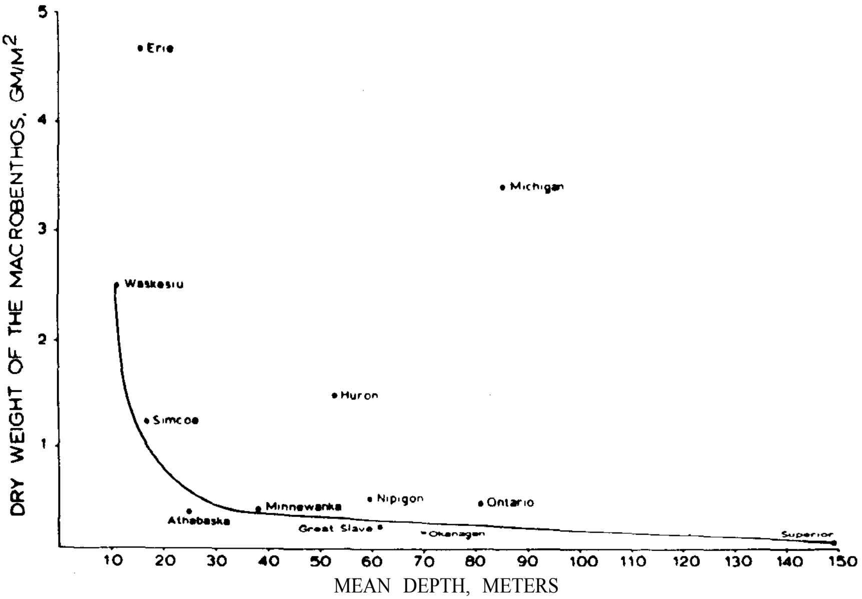

Fig. 15. Average dry weight of macrobenthos per unit area in selected lakes (from Alley

Company’s trading empire, and the distributing point for trade which extended to the Gulf of Mexico and the Pacific Ocean. As such, it boasted a population of several thousands (Bertrand, 1959). At these posts, fish, principally lake trout and lake whitefish, were a regular item of diet and, salted and packed in barrels, were distributed to less favoured posts further west. There are no comprehensive estimates of total yield from the lake but references, by travellers, to stocks of from 100 to 400 barrels of salted fish being on hand in summer (Agassiz, 1850; Bertrand, 1959) make it a reasonable guess that annual yield, all posts combined, probably lay between 500-1,000 barrels. Since a barrel weighed about 91 kg (200 lb) (Nute, 1926) this amounts to 45,400-90,800 kg (100,000-200,000 lb).

In 1835, as a subsidiary to their fur trading operations, the American Fur Company (a competitor of the Northwest Company) established a series of commercial fishing stations at the west end of the lake (Nute, 1926, 1944). Major stations were established at Grand Portage on the northwest shore, La Pointe on the southwest shore, Isle Royale, and Sault Ste. Marie at the east end of the lake. A great many minor fishing stations were also established, five more on Isle Royale for example.

Each station was staffed by fishermen and coopers, the latter making the barrels in which the fish were salted. Although seines were apparently sometimes used, the principal fishing gear was the gill net pulled by hand from small boats operating close to the stations. However, the mesh sizes employed, 15.2 cm (6 in) stretched measure for whitefish and 14.0 cm (5.5 in) for trout, were much larger than the 11.5 cm (4.5 in) modern counterpart. It is a reasonable inference that the average whitefish and trout in 1839 were considerably larger than their 1.4 kg (3 lb) modern equivalent. In August of 1835, the John Jacob Astor, a schooner of 102 metric tons (112 U.S. tons), was launched on the waters of Lake Superior. The ship carried fur, fish, and supplies between the fishery stations and Sault Ste. Marie. A year later it was felt that the fishery was being curtailed by lack of proper transportation and subsequently a scow, and two other schooners were built and launched-the *William Brewster* and the *Siskiwit.* In 1837 the company shipped 2,000 barrels of lake trout and whitefish; the yield for 1838 was 4,000 barrels and was nearly 5,000 barrels in 1839. This meant a peak harvest of virtually 454,000 kg (1,000,000 lb), a little less than a sixth of the 1941-1950 average yield of lake trout and lake whitefish combined, 2,631,000 kg (5,800,000 lb) (Baldwin and Saalfeld, 1962). Thus for a time the fishery provided a more lucrative product than furs, but the firm failed in 1842.

The postsettlement period of fisheries expansion

Following the arrival of the first settlers along the south shore of the lake in about 1850 local fisheries were established at many points on the shoreline. Initially production was largely consumed locally by the increasing population associated with the development of the copper, iron, and lumbering industries in the area, but as time passed an increasing fraction of the catch was exported to the booming U.S. midwestern cities to the south, at first by water then, as rail service in the area developed by both rail and water (Nute

1944). The scattered, and usually narrative accounts of this period provide no useful records of production, but do indicate that the nationals of both countries fished on what they regarded as the best available fishing grounds without regard for international boundaries (Quebec Legislative Assembly, 1853). The fishery was everywhere dependent upon canoes or small boats propelled by sail or oar, and the gill nets were all lifted by hand. They were also made by hand; stones were used for weights and the floats were hand-whittled. Catches not sold fresh on the local market were exported, after salting, in barrels.

Beginning in the 1870's the fisheries underwent progressive modernization of equipment and practices. In 1871, the first steam-driven vessel appeared on the lake and by 1890 some of the steamers were using steam power to lift their nets. With the increased mobility thus conferred, fisheries were extended further afield from their home ports, parties of individual fishermen being dropped off by the steamers with their small boats and gear at scattered points along the shoreline, about which small communities eventually developed, and from which the steamers routinely gathered the fish. In this way, in 1882, U.S. capital financed a fishery in eastern Canadian waters and *as* a result production increased several fold in the next decade as the extent of the operation was steadily extended northward. The fish were iced, using ice taken from the lake early in the season, packed and forwarded by lake freighter (later by rail) to southern markets (Kennedy, undated). By 1900 the modern, powered gill net lifter had been invented which permitted the use of more and longer gill nets and made deep water fishing substantially easier. Until 1930 gill nets were made of linen. Between 1930 and the 1950's linen nets were replaced first by nets of cotton and then of nylon. The latter have been shown to be 2.25 times more effective than cotton nets for catching legal-sized lake trout (Pycha, 1962) and 2.9 times more effective for taking lake whitefish (McCombie and Fry, 1960). This modernization of the fishing industry took place in both U.S. and Canadian waters, but more rapidly in the U.S. Occasionally fishermen on both sides still lift their nets by hand from small boats.

Late in this period of technological advance, Lake Superior yielded its greatest production of high valued fishes. Although the catch statistics during the early part of the period are incomplete, it appears that the total commercial catch of all species was about 1,814,000 kg (4,000,000 lb) during the 1870's, and increased to a high of 11,566,545 kg (25,500,000 lb) in 1941 before declining to the present level of about 3,629,000 kg (8,000,000 lb) (Fig. 16). Major changes in the species composition of the catches occurred during the fishing up process as the fishery developed. At its outset, as in the past, lake whitefish and lake trout dominated production but by 191.5 had yielded pride of place (in weight but not in value) to the lake herring *(Coregonus artedii* LeSueur) which has remained the dominant species to the present. Similar shifts in the relative importance of lesser species have also occurred. To a considerable extent these changes have reflected changing market demands or other economic factors but as early as 1870 there were frequent reports of the actual depletion of local supplies of fish (Milner, 1874; Nute, 1944) which resulted in the transfer of effort to less affected species

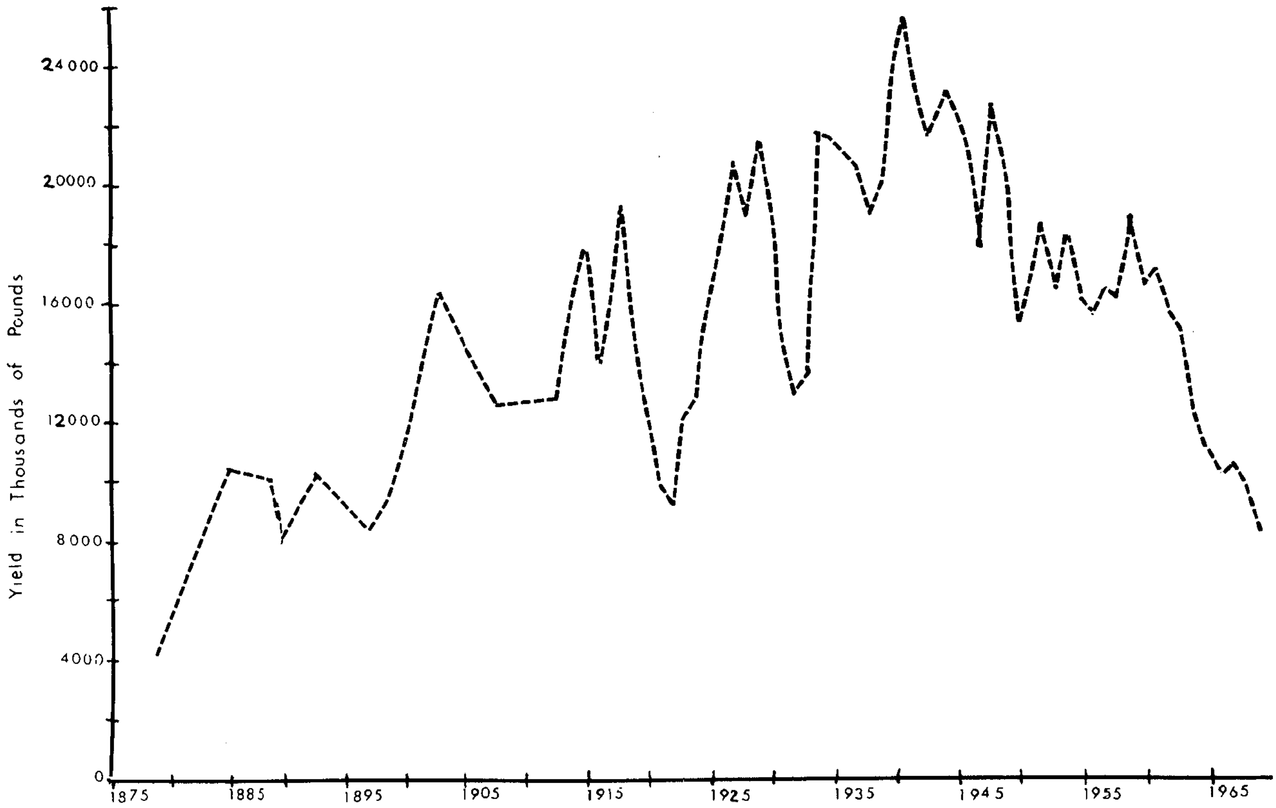

Fig. 16. Total annual yields of commercially valuable fish from Lake Superior 1885-1968 (redrawn from an original prepared by Dr. Stanford H. Smith).

The collapse of the fisheries

The period of expansion for both commercial and angling fisheries came to an end early in the 1950's at the time of the invasion of the lake by the sea lamprey (**Petromyzon** marinus L.). The movement of this predator into the upper Great Lakes, including Lake Superior, has been extensively documented (Creaser, 1932, Hubbs and Pope, 1937; Shetter, 1949; Applegate, 1950; Lawrie, 1970) and its capacity for the total extermination of cohabiting lake trout populations demonstrated (Hile, 1949; Hile, Eschmeyer, and Lunger, 1951a, 1951b; Fry, 1953; Eschmeyer, 1957a, 1957b; Fry and Budd, 1958). The first report of the species in Lake Superior waters was in 1946, and a steep and continuing decline in lake trout production set in some 5 years later. Because of the great importance of the lake trout in determining the dollar value of the catch (since it is a premium species and commands a high price) the loss of this resource was an economic disaster for the fishery, which has largely withered away despite the redirection of effort toward other, formerly less sought after species, particularly the chubs (the deep dwelling species of the genus Coregonus). In support of the fishery a program of sea lamprey control was initiated on Lake Superior in 1953; initially by operating electrical barriers to the upstream migration of spawning adults with the objective of throttling lamprey reproduction, and eventually by the application of a selective toxicant, 3-trifluormethyl-4-nitrophenol (TFM), to the natal streams to destroy the larval populations.

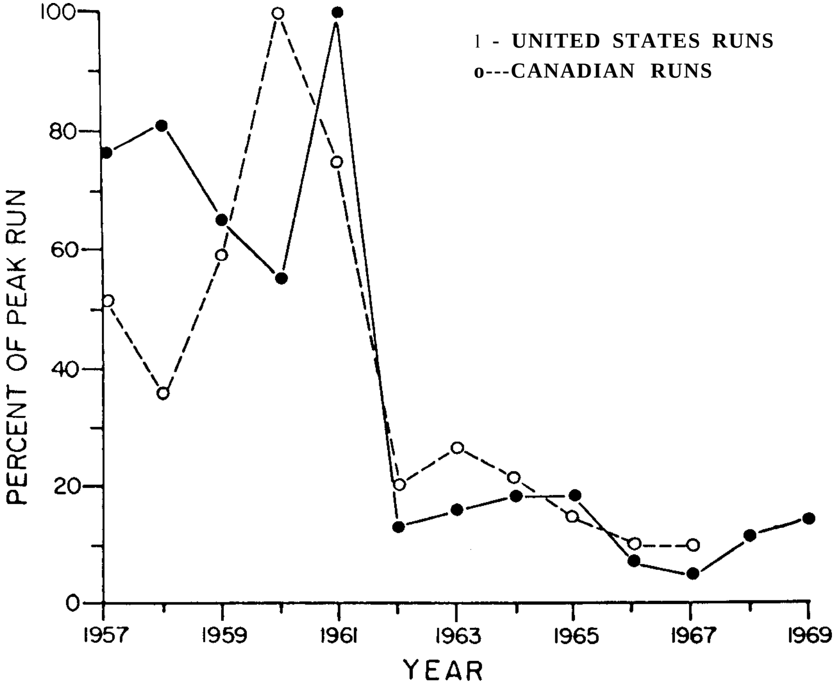

Fig. 17. Sea lamprey spawning runs at Lake Superior index electrical barriers, 1957 to 1969, expressed as percentages of the peak runs (from Lawrie, 1970).

The success of these measures has lately been reviewed by Lawrie (1970) and B. R. Smith (1971). Although the program has achieved significant success, sea lamprey are still present in the lake at somewhere between a fifth and a tenth of their former abundance (Fig. 17), and they appear still to be responsible for a serious depression in the standing crop of lake trout and whitefish. Accordingly, the fisheries remain in a depressed state.

Reasonably reliable and comprehensive annual yield statistics are available for most species for the past 55 to 70 years (Baldwin and Saalfeld, 1962). For some they extend back a further quarter century in desultory fashion. Unfortunately, however, the corresponding effort statistics have not often been published in a form which permits computation of catch-per-unit-effort estimates for individual species, or of abundance indices derived from them. Nor are there more sophisticated estimates of stock densities available from marking experiments. In consequence interpretations of yield statistics for individual species are, of necessity, largely matters of inference based, not only on the records of harvest, but also on existing knowledge of the life history of the species concerned and the behaviour of the fishery for it.

Lake trout

This species is almost universally distributed from the littoral to over 183 m (100 fath); atop every offshore shoal arising from deep water and isolated from the littoral; and even, at least as a spawner, in tributary rivers. In this diverse environment many local and apparently discrete populations of native lake trout can be recognized as morphological and/or behavioural variants. Others can be inferred from the movements of marked fish, native or planted.

Lake trout variants

Currently, commercial fishermen and buyers recognize, and assign different monetary values to, at least four variants, ***lean*** trout, ***fat*** trout (siscowet), ***halfbreeds,*** and ***humpers*** (bankers). Further there is general agreement that other variants not now extant were the objective of specific fisheries in the period before the decimation of the lake trout stocks by sea lamprey predation. Individual lake trout are often not easily assigned to one or other of the above categories and there is no doubt that in practice the sorting by commercial fishermen is always in favour of the higher price. Nonetheless these variants are sufficiently distinct in many respects to warrant individual consideration.

Two of the variants, the ***lean*** and the ***fat*** trout, are clearly distinct, at least at larger sizes, and have been accorded subspecific rank as S. n. ***namaycush*** and S. n. ***siscowet.*** These are the characteristic forms of inshore shallow waters and offshore deeper waters respectively. The former occurs normally in depths less than 73 m (40 fath) with a mode in the bathymetric distribution near 37 m (20 fath). The latter is normally taken below 91 m (50 fath) with a mode in the vicinity of 128 m (70 fath). The two subspecies show significant differences in morphology (Khan and Quadri, 1970; Lee 1971; Crawford, 1966), the ***lean*** being decidedly salmon-like in appearance, the fat having a deep, stout body and small head giving an altogether dumpy appearance. As the two common names imply there is a substantial difference in the amount of fat in the tissues, from 32.5 to *88.8%* in *fats* and from 6.6 to 52.3% in *leans,* the higher fat content having an adaptive significance in buoyancy regulation (Crawford, 1966). For both, the fat content increases with size but the regressions of percent fat on total length are obviously significantly different (Fig. 18; Eschmeyer and Phillips, 1965). Lean trout characteristically spawn between late September and early November on gravelly beaches and rocky shoals in shallow waters from 2 to 37 m (1 to 20 fath) (Eschmeyer, 1955) and some populations of *lean* trout, now apparently extinct, ascended the lower reaches of certain of the north shore tributaries for as much as two miles in order to spawn (Loftus, 1958). *Fat* trout on the other hand spawn over a much longer season and much deeper, from at least July to November depending on geographic location, in depths from 91 to 146 m (50 to 80 fath) (Eschmeyer, 1955).

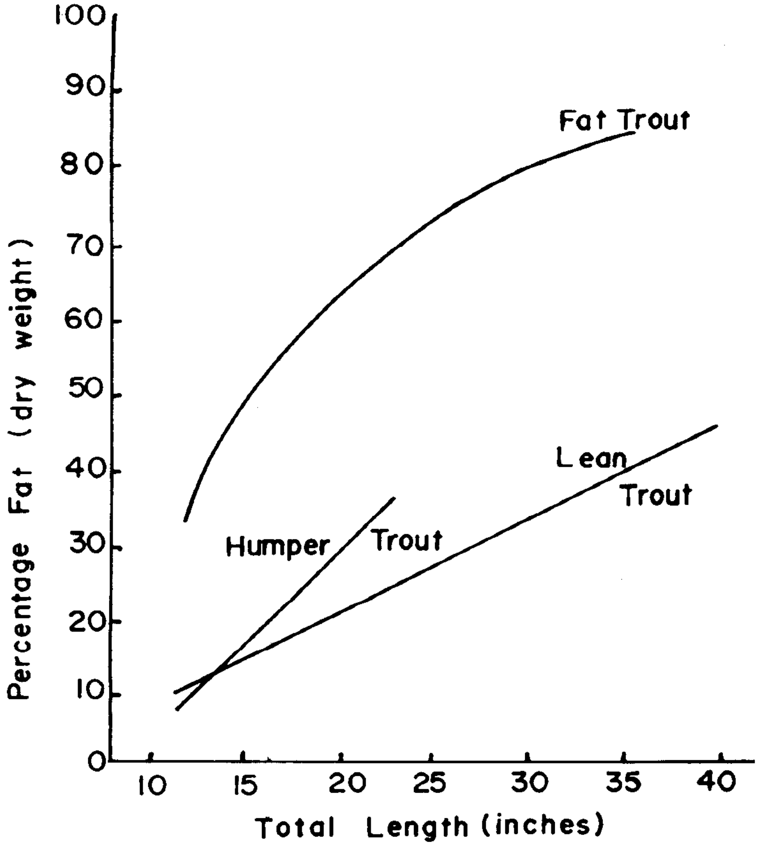

Fig. 18. The percentage fat in the flesh of three variants of lake trout from Lake Superior (after Eschmeyer and Phillips, 1965).

Although the bathymetric segregation of these two forms is not total they appear to be reproductively isolated. It is, however, a common belief among fishermen that extensive hybridization between the two forms occurs, the so-called halfbreed being considered to be the result of this cross. The two subspecies are, of course, interfertile and Eschmeyer and Phillips (1965) report on the fat content of both fat and *lean* trout and their F, hybrids which were held under essentially similar conditions in hatchery ponds. The parents displayed the expected difference in fat content and the hybrids were intermediate between them. However, the regression of fat content on length for *halfbreed* trout *from the lake* is not significantly different from that for fat trout. Khan and Quadri (1970) found no significant difference in the morphometry of fat and *halfbreed* trout nor significant differences in their meristic counts except for those of branchiostegal and anal fin rays. *Halfbreed* trout are generally smaller than those unequivocally’ classified as *fats* by the industry. They are commonly taken in depths which lie within the deeper part of the lean trout range close to the upper limit of fat trout bathymetric distribution. This suggests that *halfbreeds* may reasonably be considered to be small fats not yet large enough for their divergence in morphometry to have become sufficiently obvious to readily distinguish them, a conclusion implicit in the discussions of Eschmeyer and Phillips (1965) and Khan and Quadri (1970).

The fourth variant, *humpers,* have been described as deep bodied fish with a thin abdominal wall, a short head and a convex snout (Rahrer, 1965). These are the lake trout of the tops of offshore banks (shoals) which are separated from one another and from the inshore bank by deep water, usually of 90 m (50 fath) depth or better. Although some *humpers* are taken as deep as 110 m (60 fath) the majority, like *lean* trout, are taken in depths of less than 73 m (40 fath). Further, again like *lean* trout, they appear to spawn on their isolated reefs in water as shallow as 18 m (10 fath). Thus they appear to be largely segregated from the deeper dwelling *far* trout populations. They are, on the average, small, slow-growing trout. In fact they appear to be the slowest growing of all the Lake Superior trout stocks yet studied (Rahrer, 1967). This slow rate of growth is coupled with a tendency toward early maturity (Table 8) so that *humper* trout reproduce at substantially smaller sizes than any of the other variants considered.

Khan and Quadri (1970) regarded the *humpers* as constituting a distinct group but hesitated to comment further. Despite a passing resemblance to a small *fat* trout or a *halfbreed,* they more nearly resemble *lean* trout in their fat content (Fig. 18), in their bathymetric distribution, and in the depth at which they spawn. Their slow growth and early maturity, like that of the planktonivorous lake trout of certain Algonquin Park lakes (Martin, 1966, 1970), may simply reflect their invertebrate diet *(Mysis relicta* L. and gammarids) for forage fish are so scarce on some of these grounds, Superior Shoal for example, that cannibalism has even been reported (J. C. Budd, personal communication). Older *lean* trout tend to become pelagic, particularly during the summer months when they can be taken by the use of floating gill nets and hook lines as well as by trolling (Roosevelt, 1865; Milner, 1874; Eschmeyer, 1957a; Dryer et al., 1965; Rahrer, 1967). At least some of them appear to wander extensively as shown by tagging studies

Table 8. Ages and total lengths (mm) of Lake Superior lake trout at maturity. (Lengths given are not mean lengths at the associated age.) Lengths in inches in brackets.

Variant	Males		Females	
	Age	TL	Age	TL
Humpers[a]				
1st Maturity at	VI	323(12.7)	VI	373(14.7)
All Mature by	VII	404(15.9)	VIII	485(19.1)
River spawning *leans*				
Dog River 1952b				
1st Maturity at	VI	457(18)	VII	533(21)*
All Mature by	VII	533(21)	VIII	610(24)*
Montreal River 1951-52b				
1st Maturity at	VI	584(23)	VII	635(25)*
All Mature by	VII	635(25)	VIII	711(28)*
Lake spawning *leans*				
1950-1953 sample[c]				
1st Maturity at	VII	559(22)	IX	647(26.5)
All Mature by		737(29)	-	787(31)
1957-1966 sampled				
1st Maturity at	IV	520(20.5)	V	596(23.5)
All Mature by	-	-	-	-
Fat trout[c]				
1st Maturity at	-	-	-	S82(22.9)
All Mature by	-	-	-	-

[a] Rahrer (1965)
[b] Loftus (1958)
[c] Eschmeyer (1955) and Rahrer (1967).
[d] Dryer and King (1968).
*Fork rather than total length.

(Eschmeyer, Daly and Erkkila, 1953; Eschmeyer, 1955; Loftus, 19.58; Rahrer, 1968). Further, they *are* taken on offshore banks in small numbers, especially where the bank is relatively shallow as on Superior Shoal. It is a reasonable assumption that these offshore banks have been colonized by wandering lake trout of the *lean* type at some time in the past and the resulting populations, being essentially reproductively isolated, have undergone a considerable degree of differentiation as well as being phenotypically altered by the direct influence of the limiting food supply to yield the *humper* variant.

Lake trout movements

The movements of lake trout in Lake Superior are quite variable and range from almost zero to over 483 km (300 mi). The variability appears to be associated with: differences between variants; differences between mature and immature fish; and, in the case of hatchery-reared fish, differences in the time since release; the location of the planting site, especially in its relation to prevailing currents, and the trout densities already prevailing.

The *humpers* appear to move very little. Limited tagging experiments with this variant were conducted at Isle Royale, Caribou Island, and Superior

Shoal. Recaptures showed no significant movement to the shore banks, or to contiguous reefs, even over an extended period of time (U.S. Bureau of Sport Fisheries and Wildlife, unpublished data; Fisheries Research Board of Canada, unpublished data).

The movement studies of native *lean* lake trout (including river-spawning lake trout) and hatchery-reared, planted *lean* lake trout indicate that most fish live within a radius of about 81 km (50 mi) of their points of release or planting. However some individuals wander extensively.

Lake trout tagged in the Apostle Island area of Lake Superior in 1951-1952 were nearly all recaptured within 81 km (50 mi) of the point of release (Eschmeyer, Daly, and Erkkila, 1953). The smaller lake trout moved less than the larger ones. All recaptures of the 229-404 mm (9.0-l 5.9 in) size group were taken within the 81 km (50 mi) zone, as were 95.2% of the recaptures of the 406-506 mm (16.0-19.9 in) group, and 72.2% of those 508-785 mm (20.0-30.9 in). At least 9% of the returns, however, showed movements of over 161 km (100 mi) and three fish had moved over 410 km (255 mi).

Loftus (1958) reported that recaptures in the lake of river-spawning lake trout were mostly within 48 km (30 mi) of the spawning rivers. Only 4% of the returns were between 48 and 113 km (30 and 70 mi) of the river. However, one fish was reported captured in southern Lake Michigan, a trip involving 644 km (400 mi) through parts of Lake Superior, the St. Mary’s River, Lake Huron and most of Lake Michigan.

Buettner (1961) reported the movements of hatchery-reared, *lean* lake trout planted in Minnesota, Wisconsin, and Michigan waters of Lake Superior in 1955, 1956, and 1957. Of the recaptures reported during the first 23 months after release, 91.5% were within 8 1 km (50 mi) of the planting site. The distance to point of recapture increased irregularly with time since release. The average time at large was 7.2 months for those fish recaptured within 40 km (25 mi) of the planting site, 15.7 months for recaptures 122 to 161 km (76 to 100 mi) from the site and 26.3 months for those fish travelling over 322 km (200 mi).

Pycha, Dryer and King (1965) reported the movements of hatchery-reared, finclipped, *lean* lake trout planted in Wisconsin and Michigan waters between 1954 and 1961. They found the highest abundance of planted trout within 3-6 km (2-4 mi) of the planting site even after 3 years at large. The direction of movement closely followed the reported lake currents with the greatest dispersal in areas of strong currents and only limited movement in regions of weak currents or eddies. Very high densities of planted trout have been created in many areas in recent years; simultaneously increasing numbers of the fish seem to be moving. Whether the movement results from crowding is, however, not yet clear.

The movements of mature lake trout have been reported on and a “homing” behaviour for such lake trout from Lake Superior suggested by a number of authors (Eschmeyer, Daly, and Erkkila, 1953; Eschmeyer, 1955; Loftus, 1958; and Rahrer, 1968).

Evidence of homing to a natal area as demonstrated for Pacific salmon is almost entirely lacking. The only suggestion of such comes from observations of hatchery-reared, planted trout. Wisconsin fishery workers have noted that mature fish of hatchery origin, planted earlier from shore, tend to return to the vicinity of the beach planting sites to spawn even though there are many rocky reefs formerly used by native lake trout in the immediate vicinity. A number of hatchery-reared trout in spawning condition have even been captured in the tributary stream which flows through the hatchery where the Wisconsin fish were raised. One finclipped lake trout planted in Wisconsin waters was recaptured near southern Isle Royale 161 km (100 mi) from the planting site, tagged and released. When recaptured the second time it had returned to the vicinity of the planting site and was in spawning condition. However, many of these hatchery-reared trout have not returned to the beach planting sites and have been captured in spawning condition on grounds formerly frequented by spawning, native lake trout. The spawning sites furthest from the planting site are less used than the closer ones.

A good deal of circumstantial evidence has accumulated which infers that lake trout, having once spawned at a particular ground, will return there to spawn in subsequent years. It has also been shown that some of the trout tagged on certain spawning grounds travel great distances before recapture. However, it is not known if these fish would have returned to the spawning ground if they had not been caught. Eschmeyer, Daly, and Erkkila (1953) reported that returns from mature lake trout released near Keweenaw Point varied from recaptures at the point of release to 306 km (190 mi) away with some tendency to be nearer the points of release as the spawning season approached. Eschmeyer (1955) reported a similar tendency for fish tagged on a spawning ground at Marquette. Fully 75% of the recaptures during subsequent spawning periods were from the grounds on which they were released. Loftus (1958) stated that some river-spawning lake trout were recaptured in their respective rivers in as many as four subsequent spawning seasons. None of the fish tagged in either the Dog or Montreal Rivers ever strayed to the other river even though there was some evidence of limited mixing in the lake. The river-spawning populations also appeared to be discrete from the lake spawners as none of the river fish were captured in the lake during the spawning period. Rahrer (1968) reported that recaptures of lake trout tagged at one Wisconsin spawning ground (Apostle Island area) occurred at points from less than 8 to 193 km (5 to 120 mi) from the spawning site, but most of the returns were within 40 km (25 mi) with one recapture from over 483 km (300 mi). The mean distance to point of recapture suggests that the fish dispersed from the shoal after spawning and then returned the following year. The first month after spawning the mean distance was 5 km (3.1 mi), in months 2 to 5, it was 15 km (9.6 mi), in months 6 to 9, 53 km (33.0 mi), month 10, 26 km (16.1 mi), month 11, 9 km (5.8 mi), and by the 12th month the mean distance was 0.3 km (0.2 mi). All recaptures during the spawning season were from the tagging site although other spawning sites within 11 km (7 mi) were sampled. A few trout which had been recaptured at this site were displaced a distance of about 40 km (25 mi) and then released with sonic tags. The tags were either lost or the fish exhibited only aimless movements until the transmitter failed. One of these fish was recaptured at the original spawning site the following year.

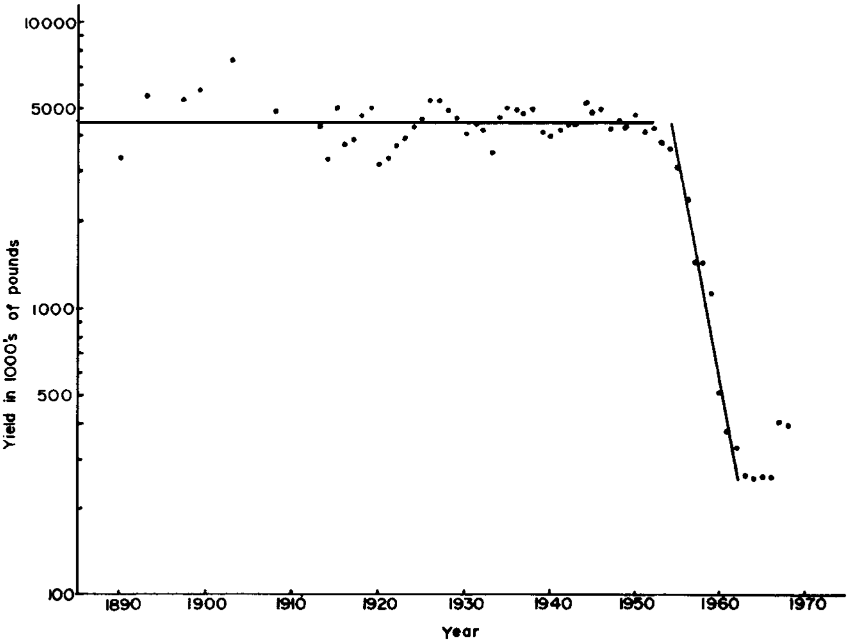

Fig. 19. Annual yields of lake trout from Lake Superior, 1885-1968.

Lake trout yields

The collection of lake trout catch statistics was somewhat irregular prior to 1913. Yield data for the entire lake are only available for 8 of the 28 years 1885 to 19 12 inclusive. Among them is the maximum recorded yield 3,334,811 kg (7,532,000 lb) in 1903. Broadly speaking there appears to be no significant long term trend in yields until 1953 (Fig. 19) when a very steep exponential decline set in at a rate of virtually 27% a year and lasted until 1962. The constant yields from 1962 to 1966 and the sharp increase in 1967 and 1968 cannot be regarded as comparable to the remainder of the series since they were taken after the fisheries were sharply restricted in 1962 and yields controlled by the application of de facto quotas.

Vying closely with the lake whitefish for first place as a table fish, usually produced in larger quantity, and cherished by the angler, the lake trout was the most important species in Lake Superior until its collapse. There is no doubt that throughout the entire history of the successive fisheries it was sought with diligence, persistence, and skill. In these circumstances the long maintenance of high yields presumably owes much to the species' widespread distribution in a multitude of quasi-discrete stocks which lent themselves to a sequential fishing-up process during the development of the fishery.

On the other hand, while acknowledging this, Hile, Eschmeyer and Lunger (195 lb) document an increase in effective fishing effort over a large part of the lake during the 1930's and 40's and thus provide convincing evidence that average stock densities were then falling despite the constant yields. Fig. 20 employs their abundance indices for stocks in the State of Michigan's waters, updated to 1953 (Great Lakes Fishery Commission Annual Report, 1958), to demonstrate that this decline, though obviously irregular and even, perhaps, cyclic, can be approximated by a negative exponential with a rate of about 2% per year.

Contributing to this excessive exploitation, at least in shallower waters, was the development of a commercial angling fishery in the second quarter of this century. Angling was probably one of the first methods used to catch lake trout. Early accounts of Lake Superior mention the ease with which lake trout could be taken by trolling with baited hook or artificial lure, sometimes attached to the canoe paddle (Agassiz, 1850; Herbert, 1851; Roosevelt, 1865; Brown, 1876). It was not, however, until 1926 that sport fishing for lake trout became something more than an individual pastime. On July 11 of that year, William "Uncle Billy" Brown tried trolling for lake trout off the south

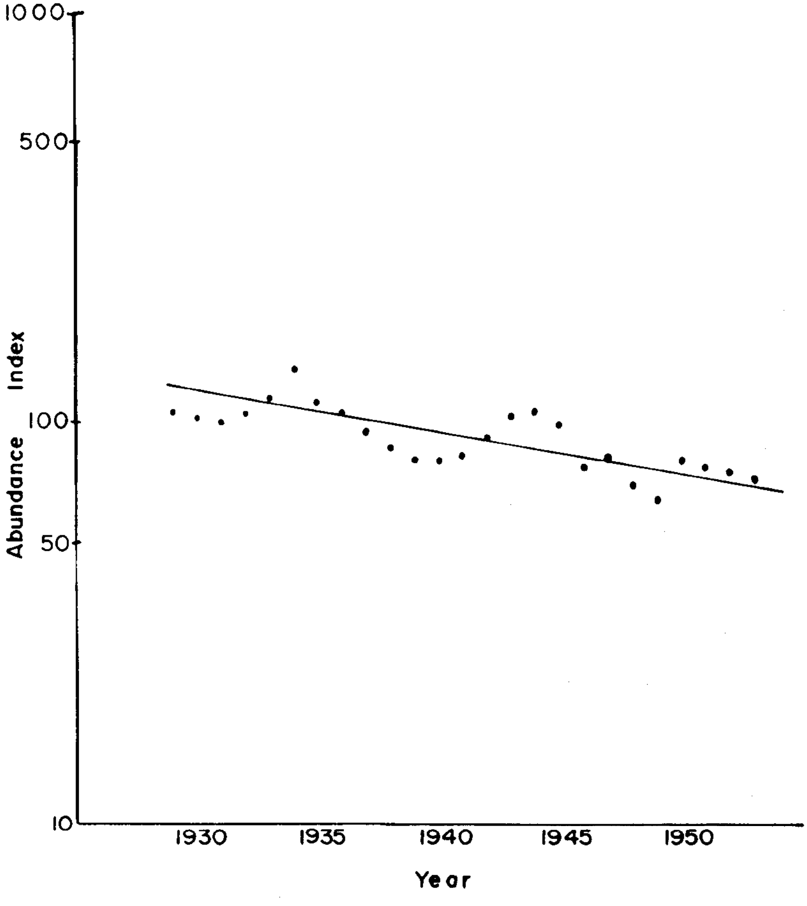

Fig. 20. Annual abundance indices for lake trout from the Michigan waters of Lake Superior 1926-1953 (updated from Hile, Eschmeyer and Lunger, 195 lb).

shore near Munising, Michigan, in the same manner he had used trolling for salmon on the West Coast. This first attempt was successful, as he is reported to have caught 649 kg (1,430 lb) of lake and rainbow trout in 5 hours (Ver Duin, undated). Whether or not this was the first modern attempt at trolling, "deep-sea trolling" was soon recognized as an effective method of catching lake trout. At virtually every U.S. port small fleets of relatively commodious and seaworthy pleasure craft or commercial fish tugs were busy during the summer months taking parties of anglers out to troll for lake trout. The trolling was highly successful with catches large enough that a common arrangement saw the first 45 kg (100 lb) of catch go to the anglers, the remainder being marketed commercially. Although the commercial portion of such catches are included in the recorded yields (the troll-caught yield amounted to an average 39,000 kg (86,000 lb) from U.S. waters between 1944 and 1950) no records are available of the purely sporting catch. In 1950, there were an estimated 47 part-time and 10 full-time charter boat operations in Canadian waters. The angling catch of this charter fleet cannot be assessed but one set of records available from Mr. Michael Krezek who operated two charter boats at the mouth of the Montreal River show the catch of the "Carol K" alone to have been 324 lake trout and a number of rainbow and "speckled" trout in 1949. Other scattered Canadian boat records show annual catches of this same order.

The effects of sea lamprey predation

As noted earlier, the sharp decline in yield which set in about 1953 coincided with the dispersal and rapid increase in abundance of the sea lamprey in Lake Superior. There is evidence to show that this predator selects larger and hence older lake trout (Fry, 1953; Fry and Budd, 1958; Budd and Fry, 1960) and the decline of the Lake Superior lake trout stocks was characterized by a progressive truncation of the upper end of both the size and age distributions and ultimately by the loss of spawners. As' control was achieved (Fig. 17) these distributions extended upward again and spawning was resumed (Dryer and King, 1968). A running summary of the progressive application of control measures and of the response of trout stocks to their success can be found in the Annual Reports of the Great Lakes Fishery Commission (1956-1969) which has directed these activities.

Although the successes of the sea lamprey control program confirmed the dominant role of the species in determining the survival of lake trout stocks it did not provide quantitative estimates of the magnitudes of the mortalities inflicted by the lamprey at various stages in the cycle of decline and recovery. The possibility of providing them by inference from the statistics of the occurrence of the wounds and scars borne by the survivors of attack is currently being investigated.

A wound is here broadly defined as a mark, caused by sea lamprey attack, which is still open and bleeding; a scar as a -mark which has at least begun to heal. A wound thus represents a current attack and wounding rates may reasonably be considered instantaneous. However, because a scar may vary from a barely sealed wound to a rescaled, hardly perceptible mark, scarring rates are cumulative functions of attack. Routine observation of both

U.S. and Canadian commercial catches has provided a comprehensive record of the frequency of occurrence of lamprey marked lake trout extending back to the late 1950's and, in desultory fashion, beyond. The usual parameters estimated from these data have been the proportion of the lake trout bearing wounds and/or the mean number of wounds per fish. The individual estimates have clearly depended on the location from which the samples were drawn, the season of the year and, since both statistics are positively correlated with prey size, on the size of the lake trout concerned. Fig. 21 shows, for Canadian waters, the year to year changes in the mean number of wounds per lake trout based on appropriately stratified autumn data.

Because the active predators of one fall are the spawning migrants of the following spring, such data should correlate well with that from the monitoring electrical barriers the following year. In fact, in general, the correlation coefficients range between 0.70 and 0.95 depending on the stratification of the primary data. Comparison of Figs. 17 and 21 affords a case in point and the excellent agreement between these independent statistics supports the belief that the relative abundance of sea lamprey in Lake Superior has been reasonably accurately estimated during the period concerned.

These same statistics should also correlate well with measures of mortality in the trout stocks. In fact, Budd, Fry and Pearlstone (1969),

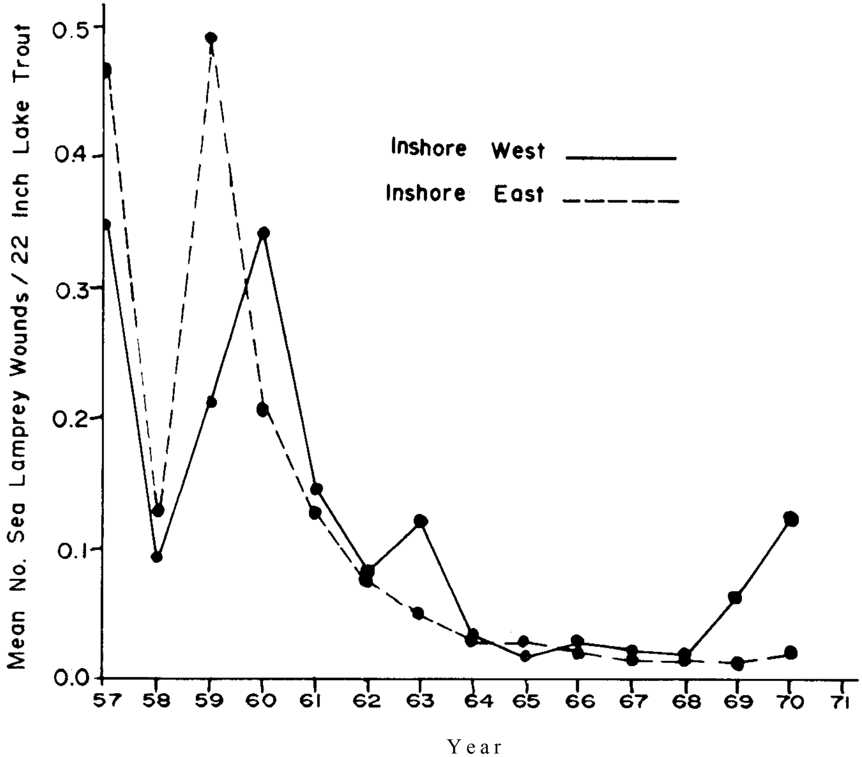

Fig. 21. The mean number of sea lamprey wounds borne by 53 cm (22 in) lake trout taken in inshore Canadian waters of Lake Superior Sept. 1-Oct. 15, 1957-1970.

discussing plantings of yearling lake trout into South Bay (Lake Huron) in the early 1950's, have reported a positive correlation between annual mortality rates and annual scarring rates at ages IV, V and probably VI. R. L. Pycha and G. R. King (personal communication) have also found a positive correlation between the total annual mortalities suffered by certain plantings of lake trout in U.S. waters and the proportion of the trout which were wounded. Similar studies are being pursued in Canada.

The effects of planting hatchery-reared lake trout

To minimize the likelihood of lamprey-induced year class failures, very large numbers of hatchery-reared lake trout were planted into the lake (Table 9) in a program complementing that of lamprey control. During the 1960's these fish increasingly dominated inshore lake trout catches until by the middle of the decade they contributed upwards of 95% of the trout taken in most areas. Further, under the more favourable mortality regime consequent on control of the sea lamprey, stock densities increased steadily by about 14% per annum from 48 fish per 3,048 m (10,000 ft) of gill net in 1962 to 140 per 3,048 m (10,000 ft) in 1969 (Great Lakes Fishery Commission, 1969). That this recovery is not fully reflected in the yield statistics of Fig. 19 is entirely owing to the imposition in 1962 of restrictions on the commercial fisheries of both the United States and Canada. The increased yields of 1967 and 1968 resulted from a 25% relaxation in those restrictions.

Lake whitefish

Unlike the ubiquitous lake trout this species is restricted to inshore, shallow water habitats. For example, in the Apostle Island area on the southwest shore it is found in depths from less than 18 to 64 m (10 to 35 fath), most fish being taken between 18 and 53 m (10 and 29 fath) (Dryer, 1966). The species has not been shown to be differentiated into morphologically recognizable variants like the lake trout. Nonetheless, available life history data, returns from tagging studies of movement and the production statistics themselves suggest that it, too, is distributed as a series of quasi-discrete stocks.

Lake whitefish life history

Growth rates of lake whitefish from five widely separated localities along the south shore of the lake were quite distinct (Edsall, 1960; Dryer, 1963). The difference in size among the stocks at the end of the first year of life, based on back calculation from the scales, was just over 25 mm (1 in) but by the end of the 7th year the difference was 300 mm (11.8 in) between the fastest growing and the slowest (Table 10).

Dryer (1963) examined the relative strength of various year classes in the commercial catches of four Lake Superior ports and stated that there was little evidence of any lake wide similarity in fluctuations of year class strength. Some of the greatest differences in relative strength of various year classes existed between the neighboring ports of Whitefish Point and Dollar Settlement.

Table 9. Thousands of finclipped lake trout planted in the four jurisdictional areas of Lake Superior.

Year	Minnesota		Wisconsin		Michigan		Ontario		Total	
	Age 0	Age 1 or Older	Age 0	Age 1 or Older	Age 0	Age 1 or Older	Age 0	Age 1 or Older	Age 0	Age 1 or Older
1947							28		28	
1948							33		33	
1949										
1950							50		50	
1951										
1952			145	102	65				210	102
1953			133	80	139	69	50		322	150
1954			142	102	121	134			264	236
1955				103		61				164
1956				201						201
1957										
1958				184		298		538		1,020
1959				151		43		473		667
1960			49	161		893	50	396	100	1,450
1961				314		392	60	494	60	1,200
1962	77			493		775		508	77	1,777
1963	38			311		1,186		477	38	1,974
1964		182		743		1,196		472		2,594
1965		102		448		827		468		1,844
1966	151	108		377		2.218		450	151	3,152
1967	154	228	105	244		2,059		500	259	3,031
1968		223		239		2,260		500		3,222
1969		216		251		1,860		500		2,827
1970		226		204		1,916		501		2,847
Totals										
Age 0	420		575		326		271		1,592	
Age 1 or older		1,285		4,709		16,188		6,275		28,457
Grand Total										30,049

Table 10. Calculated total length (in) of Lake Superior whitefish according to locality.

Year of Life	Bayfield	Marquette	Munising Bay	Whitefish Pt.	Dollar Settlement
1	5.1	5.6	5.5	6.6	5.9
2	8.0	9.0	1.2	11.2	9.5
3	10.9	12.4	8.4	14.7	12.7
4	13.3	15.6	9.4	17.6	14.8
	15.0	18.2	10.1	20.4	16.9
6	16.7	20.0	10.8	21.7	18.6
7	18.3	21.5	11.5	23.3	20.3
8	20.0	22.9	12.1		21.4
9	21.4	25.2	12.9		22.4
10	22.1	26.8	13.6		23.8
11			14.4		
12			15.4		
13			15.7		
14			16.0		
15			16.3		
16			16.7		

Table 11. Age and total length (mm) of Lake Superior lake whitefish at maturity. Lengths in inches in brackets.

Location	Males		Females	
	Age	TL	Age	TL
Apostle Islands				
1st Maturity	v	374(14.7)	V	412(16.2)
All Mature	VII	430(16.9)	VII	442(17.4)
Munising Bay				
1st Maturity	VII	297(11.7)	X	310(12.2)
All Mature	XII	366(14.4)	XII	379(14.9)

Sex ratios, age, and size at maturity data are available only from the stocks of the Apostle Island area and Munising Bay. Sex ratios of the two populations were almost equal: 5 1.5% males -Apostle Island (Dryer, 1963) and 52% males - Munising Bay (Edsall, 1960). Size and age at maturity data for the two stocks are presented in Table 11 and reflect their differing growth rates.

Lake whitefish movements

All the returns of whitefish tagged in the Apostle Island area of Lake Superior were recovered within 40 km (25 mi) of the tagging site (Dryer, 1964). Two groups of whitefish were tagged: 1,222 small whitefish, 269442 mm (10.6-17.4 in) tagged in June and July; 18 1 spawning-run fish, 406-602 mm (16.0-23.7 in) tagged in November. Of the smaller fish, nearly 65% were recaptured within 8 km (5 mi) of the tagging site and the greatest movement was 27 km (17 mi). Of the spawning-run group, over one-half (56.5%) were recaptured within 8.0 km (5 mi) of the tagging site and the greatest distance travelled was 40.2 km (25 mi). Seven of the spawning-run fish have been recaptured on the same grounds in subsequent spawning periods. Other Great Lakes workers have reported results similar to Dryer's (Smith and Van Oosten, 1940; Spangler, 1970). Budd (1957) however, reported more extensive movements for two Lake Huron whitefish stocks but noted a tendency for the stocks to remain discrete.

Lake whitefish yields

Early accounts (Agassiz, 1850; Milner, 1874; Capp, 1904; Nute, 1944; Warren, 1957; Kennedy, undated) make it clear that, in the Lake Superior basin as elsewhere in its range, the whitefish was very highly prized as a table fish. It was also readily available in its shallow, inshore environment and was first fished there with seines and, by 1860, with pound nets whose numbers rapidly increased (Dryer, 1963). To exploit more remote, deeper stocks (and other species) gill nets were very quickly introduced and soon became the dominant gear (Nute, 1944). By 1885 the high point in yield, 2,348,700 kg (5,178,000 lb) had been reached. Subsequent trends in yield are shown in Fig. 22.

There appear to have been four episodes in the history of the fishery. Until 1920 yield declined at essentially 6% per annum. From then until 1955 it increased by virtually 3% a year. Thereafter a steep decline at a rate approximating 17% per annum lasted until 1960 or thereabouts only to be terminated by a rapid increase at an apparent rate of 8% per annum.

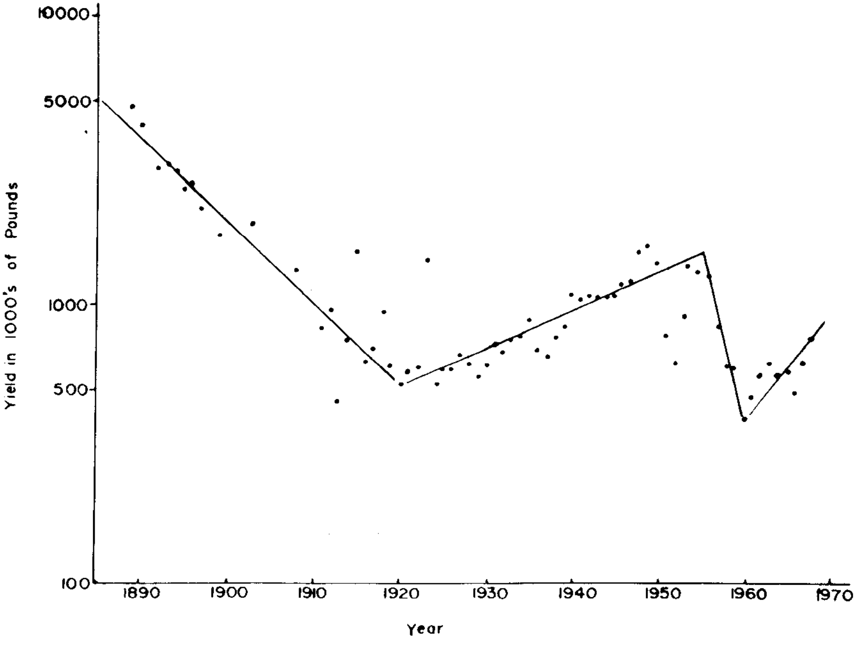

Fig. 22. Annual yields of lake whitefish from Lake Superior, 1885-1968.

The causes of the trends in yield described by the first two segments of the curve cannot be inferred with confidence. The initial decline is tentatively equated with the sequential fishing-up of one quasi-discrete stock after another at rates exceeding those providing maximum sustained yield. There is, however, a real possibility that the loss of many estuarine and river spawning stocks (there was once an abundant stock in the St. Mary's River at the outlet of the lake and probably others in its tributaries) resulted from the deposit of woody allocthonous materials over much of their habitat during the intense lumbering activities earlier referred to. Certainly, it was a common complaint of commercial fishermen that deep drifts of sawdust blanketed many whitefish spawning beds in the lake and they believed that these both inhibited spawning and suffocated such eggs as were deposited (Milner, 1874; Nute, 1944).

Since both lake trout and whitefish occur on inshore littoral fishing grounds in depths of less than 55 m (30 fath) (Dryer, 1966) and are commonly taken in the same nets, changes in effort statistics for lake trout should also be broadly applicable to whitefish. If so, there must have been an increase in fishing intensity for whitefish, too, between 1920 and 1955. The increasing yields coming on the heels of a long decline attributed to overfishing can only have resulted from a considerable recovery in the whitefish stocks themselves. What brought it about is not clear. It has been attributed (Nute, 1944) to the planting of artificially reared eyed eggs or, more usually, sac fry. However, since this practice was carried on through much of the preceding period of decline without apparent result, the argument is unconvincing. It may be, as already suggested in the section on lake water chemistry, that the environment recovered somewhat following the marked reduction in lumbering activities early in this century.

The trends in yield shown by the last two segments of Fig. 22 have a more obvious explanation. The precipitous decline in the late 1950's is, like the comparable change in lake trout yields, positively correlated with the rise in the abundance of sea lamprey. The demonstration by Spangler (1970), for a Lake Huron whitefish population, of a seasonal pattern of mortality which closely followed the seasonal pattern of lamprey activity supports the inference of a causal connection, as does the rapid recovery consequent on the application of effective sea lamprey control measures. There being no inhibiting restrictions applied specifically to the fisheries for whitefish, yields in this case did reflect the increase in abundance consequent on control of the lamprey (cf. Figs. 17 and 21 with 22).

The chubs and lake herring

The deepwater species of the coregonine subgenus ***Coregonus (Leucichthys)*** are commonly referred to in the Great Lakes by the collective term chubs. Five species: C. ***hoyi*** (Gill), the bloater; ***C. nigripinnis*** (Gill), the blackfin; ***C. zenithicus*** (Jordan and Evermann), the shortjaw; C. ***kiyi*** (Koelz), the kiyi; and ***C. reighardi*** (Koelz), the shortnose were recognized by Koelz (1929) as occurring in Lake Superior. Their single shallow water congener, the lake herring ***(C. artedii*** LeSueur) is the only other representative of the subgenus known to inhabit the lake.

Collectively the group is highly plastic not only in morphology but also in habits. The life history data of Table 12 has been gleaned from a variety of sources (Koelz, 1929; Van Oosten, 1937a; Moffett, 1957; Scott, 1960, 1961; Dryer and Beil, 1964, 1968; Dryer, 1966; Anderson and Smith, 1971a, 1971b) several of which treat the various species as they occur in other lakes. The tabulation should accordingly be regarded as tentative as well as incomplete.

Because of the difficulties in discriminating among these several species the commercial fishermen and the markets they serve have commonly recognized only the two groups, chubs and herring (ciscoes). Prior to 1950 even this distinction was not made in recording the yield statistics although Dr. Stanford H. Smith of the U.S. Bureau of Sport Fisheries and Wildlife has re-examined these earlier data and managed to separate the herring from the chubs. The data upon which these accounts are based were generously made available by Dr. Smith.

The chubs

Since the catches of the various chubs have never been officially separated in recording commercial yields, changes in species composition must be inferred from the available biological studies of the species.

The first major change in the chub populations of Lake Superior occurred between about 1893 and 1910. *C. nigripinnis* was probably the most desirable table fish of the lot. Koelz (1929) stated that they were in short supply in Lake Michigan in the late 1800's and that, therefore, production was shifted to Lake Superior. This large chub was fished there for about 10 years and was reported to be commercially extinct by 1907. The diary of one commercial fish tug from Marquette, Michigan showed a further decline in catch-per-unit-effort of *C. nigripinnis* from 68.5 kg per 30,480 m (151 lb per 100,000 ft) of net in 1910 to only 1.81 kg per 30,480 m (4 lb per 100,000 ft) in 1915.[1] The yield statistics (Fig. 23) show the rise and fall of *C. nigripinnis* as occurring between about 1895 and 1915. There is no evidence of anything besides the fishery which could have affected its abundance during this period.

In 1925 the Lake Erie cisco *(C. artedii)* fishery collapsed, thus increasing the demand for similar fish from other lakes. In response the Lake Superior fishery started harvesting the shortjaw chub (C. *zenithicus)* as well as increasing the harvest of C. *artedii.* Koelz (1929) reported that one lift of chub nets from the Apostle Island area in 1922 contained 300 *C. zenithicus* but only one each of *C. hoyi, C. nigripinnis* and *C. reighardi.* Van Oosten (1937a) stated that by the mid-1930's *C. zenithicus* was the only large chub common enough to support a commercial fishery in Lake Superior. The next observation on species composition does not appear until Dryer and Beil (1968) reported the composition of chub catches in 1958-1965. They stated that in the same area where Koelz (1929) observed a predominance of C. *zenithicus* the catch now consisted of 92% C. *hoyi* and only *8% C. zenithicus.* Fig. 23 shows a peak in 1927, about 2 years after the *C. zenithicus* fishery

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[1] These data from the records of the Anderson Fish Company kindly provided by Mr. R. L. Pycha, U.S. Bureau of Sport Fisheries and Wildlife.

Table 12. Some life history characteristics of the Coregonus (Leucichthys) species of Lake Superior. Depths in m (fath in parentheses). Total lengths in mm (inches in parentheses).

Item	*C. artedii*	*C. hoyi*	*C. nigripinnis*	*C. zenithicus*	*C. kiyi*	*C. reighardi*
Bathymetric Distribution	S-165 (3-90)	18-165 (10-90)	27-183 (15-100)	18-163 (10-89)	37-183 (20-100)	29-152 (16-83)
Depth of Max. Catch	18-53 (10-29)	55-108 (30-59)		55-126 (30-69)	128+ (70+)	
Food	Crustaceans, mostly copepods	Crustaceans, mostly copepods	Smelt and *Mysis*	Crustaceans, mostly *Mysis*	Crustaceans, mostly *Mysis*	Crustaceans, mostly *Mysis*
Age at 1st Maturity						
Males	I	II		IV		II
Females	II	II		IV		II
All Mature at						
Males	IV	IV		V		III-IV
Females	IV	IV		V		III-IV
Percent Female	Increases with age. (72% at IV)	Increases with age. (60% at IV)		59%	Increases with age	
Spawning Date	Nov.-March mostly Nov.-Dec.	All season but mostly Feb.-Mar.	Sept.-Oct.	Nov.-Dec.	Nov.-Dec.	May or June
Depth	1.5-128 (8-70)	37-92 (20-50)	110-183 (60-100)	18-55 (10-30)		37-145 (20-79)

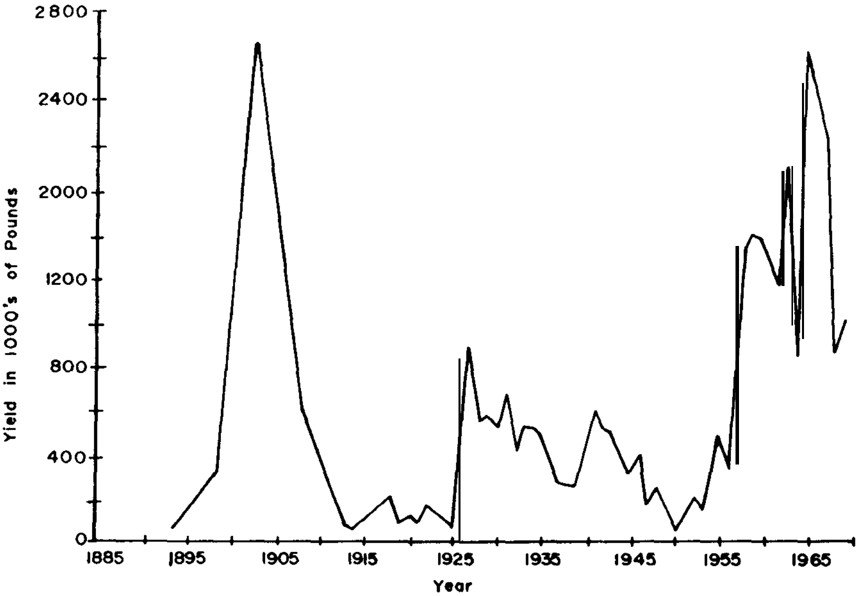

Fig. 23. Annual yields of chubs from Lake Superior, 1893-1968 (redrawn from an original prepared by Dr. Stanford H. Smith).

started, and then an irregular decline to a low in about 1950. Again exploitation by the fishery is the only apparent cause of the reduction of the C. zenithicus population in U.S. waters.

In the Canadian waters of Lake Superior, the commercial fishery has never exploited chubs except casually or incidental to other fishing. in 1971, however, an experimental chub fishery was opened and the initial observations show the species composition to comprise equal numbers of C. *hoyi* and C. *zenithicus.* This would seem to indicate an intermediate stage between Koelz's observations of the nearly unexploited phase and Dryer's observations during intense exploitation.

Although there are no records of the species composition of U.S. chub catches through the 1950's it is certain that late in that decade and early in the next they were dominated by C. *hoyi.* As the lake trout population of Lake Superior declined between 1955 and 1960, the fishery was forced to turn to other species and the increased importance of the C. *hoyi* catches is well shown in Fig. 23 (the two low values in 1964 and 1968 were caused by unfavourable markets created by cases of fatal botulism poisoning from consumption of improperly processed smoked chubs). Moffett (1957) reported a similar trend in the chub fisheries of Lake Michigan following the collapse of the lake trout fishery there during the 1940's. Thus, indirectly, sea lampreys worked to augment the intensity of the commercial chub fisheries and to accelerate their effects. On the other hand they also worked, by reducing the numbers of both the climax predators, the lake trout and the burbot *(Lota lota* Linnaeus), to reduce the natural mortality for C. *hoyi* whose populations then expanded (Dryer et al., 1965). These changes were comparable to those particularly well documented for Lake Michigan by Moffett (1957) and Smith (1964, 1968).

Accompanying the population explosion of C. hoyi was an increase in growth rate. Thus, Dryer and Beil (1968) reported that this chub grew much faster during the period 1962-1965 than in 1958-1961. In the later period fish were 28 mm (1.1 in) longer at age V and reached a length of 254 mm (10 in) two years earlier than those from the earlier period. Smith (1964) noted that C. hoyi greatly extended its bathymetric range in Lake Michigan as they became the dominant cisco and this created favourable conditions for hybridization with *C. artedii.* He made special note of a "new fish" which appeared to be a *hoyi X artedii* cross. The presence of intergrades between these same two species in current catches from Lake Superior suggest that the same introgression is occurring there.

Each of the three species which has dominated Lake Superior's chub fisheries was smaller than its predecessor. A similar sequence of progressively smaller forms was also reported from Lake Michigan (Smith, 1964). There it was attributed to the effects of an intense small-mesh gill net fishery which used progressively smaller mesh sizes to crop down the larger chubs. It is almost certain that this was also the course of events in Lake Superior. Sea lamprey predation on larger chubs was also held to significantly reinforce the effect of selective fishing in Lake Michigan (Smith, 1968). Lamprey predation cannot, however, have been a factor in Lake Superior for all but *hoyi* had already been fished to virtual extinction before the first sea lamprey was reported, in 1946. Nor did competition from alewife *(Alosa pseudoharengus* (Wilson)) play the role in Lake Superior that it apparently did in Lake Michigan (Smith, 1968) for that species entered the lake almost 10 years too late (Carlander, 1969) to have had a hand in the suppression of C. *nigripinnis* and C. *zenithicus.* Nor is it abundant enough to affect *hoyi* populations,

Lake herring

Although, as Table 12 suggests, lake herring are found through a wide range of depths they are, for a large part of the year, pelagic plankton feeders in mid or near surface waters. At such times the schools are vulnerable to small mesh gill nets drifted at or near the surface or, in shallow enough water, to nets set right on the bottom. They are especially vulnerable to these methods, or to the recently introduced trawls, in late autumn and early winter when they become aggregated in very dense schools in shallow inshore waters, or on offshore banks, preparatory to spawning (Dryer and Beil, 1964). Traditionally, about 90% of the annual catch has been taken at this time but within the past five years aggressive fisheries have been developing at other seasons as well, especially in Canadian waters.

There is no direct evidence of the existence of multiple stocks of lake herring in Lake Superior. However, tagging data from Lake Michigan (Smith and Van Oosten, 1940) showed movements of only 16 km (10 mi) on the average in that lake so that it seems likely that the population consists of many local, quasi-discrete stocks. Such an assumption is consistent with the general observation that the decline in both yields from, and abundance of, the herring stocks has not been synchronous or of equal intensity over the lake as a whole.

Records of commercial yields of lake herring begin in 1867 and the maximum yield of a little over 8,600,000 kg (19,000,000 lb) was reached in 1941 (Fig. 24) (Dryer and Beil, 1964). In general the slowness and irregularity of the growth of the fishery in the early part of the century was probably more a response to fluctuations in price and demand than to changing availability of herring. Later changes, however, may well have been related to stock depletion in various waters. At any rate the relative contribution of several areas has changed progressively and significantly. Thus, until recently most herring have been taken in U.S. waters. There, Minnesota dominated production from 1929 until 1940 to be followed between 1941 and 1956 by Wisconsin and finally, till the present by Michigan. Until 1965 the average Canadian yield of 692,632 kg (1,527,000 lb) was only 11% of the total. Now (1969) at 1,086,807 kg (2,396,000 lb), it represents 50% of the lake total.

Dryer and Beil (1964) demonstrated that a decline in average lake herring abundance (catch-per-unit-effort) of virtually 30% had, in fact, occurred in two widely separated fisheries, one in Wisconsin, one in Michigan between 1950-1955 and 1956-1961. Anderson and Smith (1971a) examined the commercial catch statistics from all western U.S. fisheries and demonstrated that for most statistical districts not only yield but abundance and effective effort have all been declining more or less steeply since 1949. On this basis they rejected overfishing as the primary cause of the post 1961 collapse and, finding no deleterious abiotic factor of general significance, concluded that competition for food with the increasing populations of bloater (C. ***hoyi)*** and particularly of the introduced smelt ***(0. mordax)*** was the most probable cause of the decline.

It is, however, possible that Anderson and Smith underestimated the role of exploitation by, apparently, failing to take into account the conversion by the fisheries from cotton to nylon gill netting during the period studied.

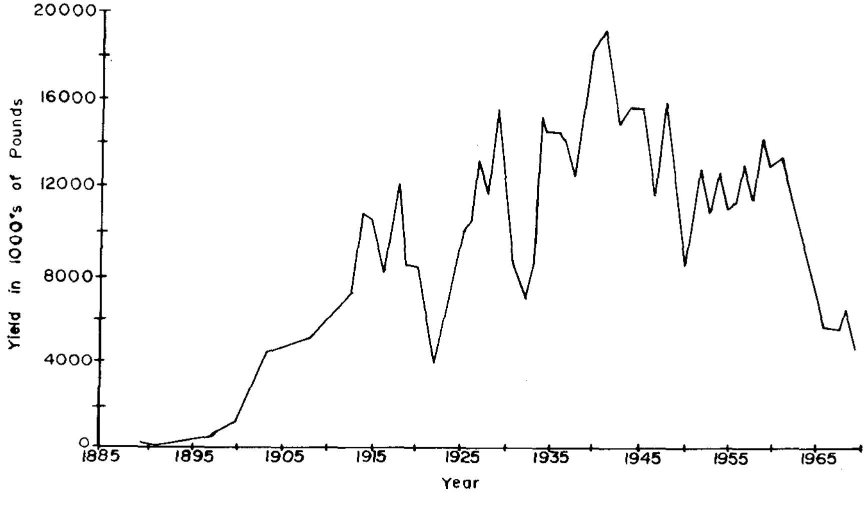

Fig. 24. Annual yields of lake herring from Lake Superior, 1889-1968 (redrawn from an original by Dr. Stanford H. Smith).

Dryer and Beil (1964) report the latter netting to be 4.3 times more effective in taking lake herring than the earlier cotton. Since the use of nylon became widespread at the end of the 1950's this omission might well invalidate the contention that effective effort had in fact declined.

There is also some reason to believe that the conventional commercial statistics may be deceiving because catch data are summarized by rather large areas. All of Wisconsin's waters are treated as a single district for example, despite the very real possibility that they may contain a number of individual quasi-discrete stocks. Personal conversations with commercial fishermen in the Apostle Island area support this view. It is stated that fishermen have repeatedly had to move their fishing grounds to new spawning areas as abundance in areas formerly heavily fished decreased. At one time the grounds fished were only a few minutes run from port. Now they require several hours to reach. In this process fishermen ill equipped for distant fishing have been eliminated, thus reducing total effort while pressure on the remaining stocks was maintained at a very high level. In this way, successive exploitation rates specific to each stock may well have been greater than those permitting sustained yields despite the decline in total effort. It is perhaps significant that depletion has been greatest where heavy fishing has been longest maintained or earliest begun.

Sturgeon, walleye, and smelt

Apart from the lake trout and coregonines only three species have ever provided a commercial yield as large as 113,397 kg (250,000 lb): lake sturgeon *(Acipenser fulvescens* Rafinesque), walleye *(Stizostedion vitreum* (Mitchill)) and the smelt (O. *mordax).*

The maximum yield of sturgeon occurred at the very beginning of the period of record, 101,605 kg (224,000 lb) in 1885 (Fig. 25). Subsequently yields declined at a rate of about 9% a year and since 1920 have exceeded 4,536 kg (10,000 lb) only three times. Because of its highly vulnerable position in the shallow waters of estuaries and adjacent inshore areas it may simply have been fished out. Certainly, with its low biotic potential (Carlander, 1969) it could hardly be expected to withstand even light exploitation. On the other hand it must, perhaps even more than the lake whitefish, have been vulnerable to the habitat destruction caused by the driving of rivers and the discharge of woody allochtonous materials during the heyday of the pioneer lumbering industry (Harkness and Dymond, 1961).

Walleye are largely absent from the open lake but have supported intense but highly local fisheries in the warmer waters of the shallower large bays and island regions. Usually they have been associated with particular rivers. Those in U.S. waters have been relatively unimportant since the first decade of this century with an aggregate yield, at best, of less than 34,019 kg (75,000 lb). Those in Canadian waters provided a peak yield of 171,004 kg (377,000 lb) in 1966. Ryder (1968) has provided evidence suggesting that elimination of one of the two principal stocks in Canadian waters was probably owing to local industrial pollution originating from a kraft process paper mill located immediately downstream from its principal spawning ground in the estuary of the Nipigon River. The other stock, though largely

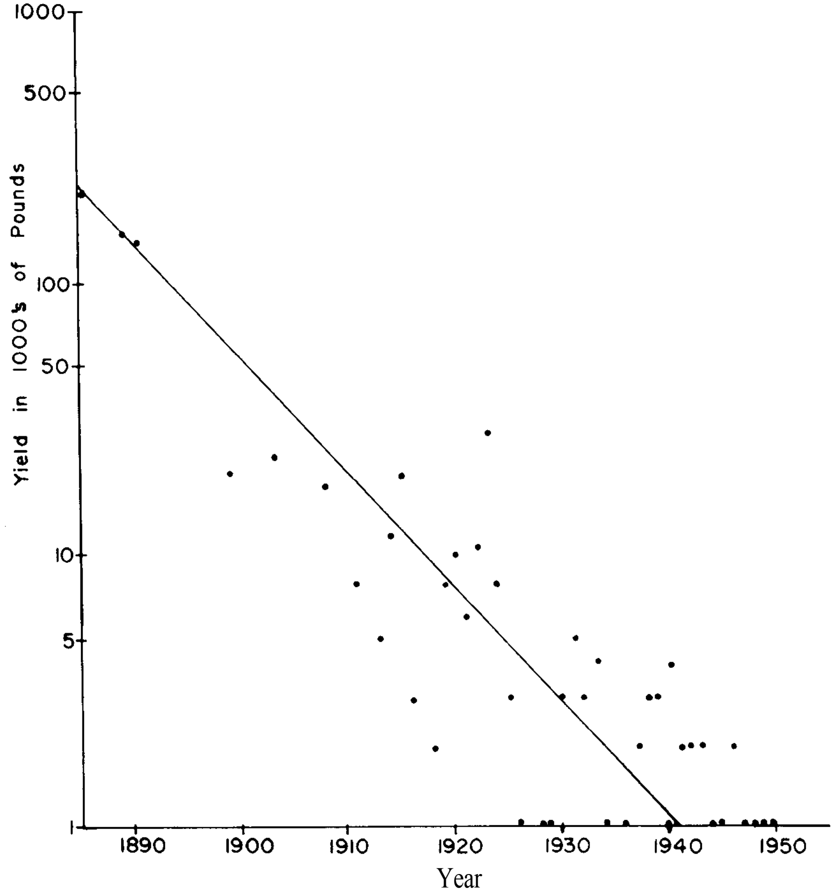

Fig. 25. Annual yields of lake sturgeon from Lake Superior, 1885-1950.

responsible for the peak yield of 1966, is also in trouble and the 1969 yield was only 10,622 kg (23,417 lb). The causes of the decline are not yet clear.

Smelt, like sea lamprey, are immigrants to the lake, being first recorded there in 1930 (McKay, 1963). Systematic commercial harvesting began in 1952 when the recorded yield was 20,412 kg (45,000 lb). Yields, almost entirely from U.S. waters, rose exponentially at a rate of almost 40% each year until 1961. Since then they have fluctuated around a mean of 636,844 kg (1,404,000 lb) annually. Reference has already been made to the role of this species as a competitor with lake herring and bloaters for available food. Berst and Spangler (1972) infer that it may have played an analogous role in constraining whitefish production in Lake Huron. On the other hand it has clearly supplanted the chubs as the principal food of Lake Superior's lake trout population (Dryer et al., 1965) and presumably plays an important role as prey for the other piscivorous salmonids: speckled, rainbow, and brown trouts *(Salvelinus fontinalis* (Mitchill), *Salmo gairdneri* Richardson, and *Salmo*

trutta (Linnaeus)) and coho and chinook salmon ***(Oncorhynchus kisutch*** (Walbaum) and ***Oncorhynchus tshawytscha*** (Walbaum)).

Introductions to Lake Superior

It is certain that throughout the century and a half that Lake Superior's fisheries have been exploited there have been repeated attempts to augment natural reproduction by the planting of hatchery products, or to introduce exotic species to the drainage. It is, however, a particularly intractable problem to attempt to provide a record of these introductions, for the plantings have been made by many jurisdictions who have recorded their activities in different, and often changing formats, and who have, too often, had little concern for the maintenance of long-term coherent records. On the Canadian side of the lake the Ontario Ministry of Natural Resources, who are now attempting to document the history of the Province's activities in this regard, have found it difficult to assemble reliable records extending much further back than 1946 (K. Chambers, personal communication). Whether comparable efforts have been, or are being made, by jurisdictions on the U.S. side of the lake is not known However, no general statement of the plantings into U.S. waters is currently available (John Appleget, personal communication).

Nonetheless, it is clear that extensive plantings of hatchery stock, either as eyed eggs, fry, fingerlings, or yearlings have been made. For example, between 1922 and 1946, with the exception of a single year, somewhere between 200,000 and 32,820,000 lake trout (usually as eggs, fry, or fingerling) were planted annually into the Canadian waters of Lake Superior. Similarly, during the same period of time and with the exception of four years only, plantings (usually of eyed eggs or fry) numbering between 540,000 and 70,375,000 lake whitefish were planted into these same waters. In 14 of the years walleye ***(Stizostedion*** vitreum (Mitchill)) were planted in numbers ranging from 23,000 to 20,000,000. Brook trout ***(Salvelinus fontinalis*** (Mitchill)) were planted in four years, usually in numbers under 10,000 but in one year the records indicate that 5,800,000 trout (at some stage in their life history) were planted. That there is little sign of benefit from these activities has been indicated by Dymond (1957) in a review of the role of artificial propagation in the management of Great Lakes fisheries.

On the other hand, the introductions of certain species have unquestionably been successful. Those of yearling lake trout, planted to complement the sea lamprey control program, have already been referred to. Two exotic salmonids have also become established in the lake as a result of deliberate stocking and two others are currently being maintained on a put-and-take basis. Rainbow trout ***(S. gairdneri*** Richardson) were first stocked into Lake Superior in 1895, apparently as eyed eggs, and were well established as spawning residents on both sides of the lake within 10 years (McKay, 1963; Bidgood and Berst, 1967). Severely reduced by sea lamprey predation, they have been recovering rapidly since 1962 with the support of modest plantings of yearling fish, especially in U.S. waters. Much sought after by anglers they promise to be even more important in the future in the economy of the lake. Brown trout ***(S. trutta*** Linnaeus) were introduced to U.S. waters (as eyed eggs?) at about the same time as rainbow trout and like them have established spawning populations especially in southwestern Lake Superior (Scott, 1967). Populations are currently expanding and being supported by modest plantings of yearling trout. Stray adults occur in Canadian waters but have not apparently spawned there. Coho salmon (Oncorhynchus kisutch (Walbaum)) were introduced in 1966 (Peck, 1970) and have been stocked into U.S. waters each year since in steadily increasing numbers which reached 660,000 smolts in 1969 (Great Lakes Fishery Commission, 1970). Only small numbers have been stocked in Canadian waters. The results have been much less spectacular than those obtained in Lake Michigan (Wells and McLain, 1972) although an active angling fishery has developed. Total survival of the first three plants has been erratic and below values for the same year classes in Lake Michigan; 12, 2, and 24% in Lake Superior (Great Lakes Fishery Commission, 1969) compared to 32, 19, and 25% in Lake Michigan (Wells and McLain, 1972). Reflecting Lake Superior's lower productivity, growth has also been much slower than in Lake Michigan. The average weight of returning Lake Superior spawners was 1.3 kg (2.9 lb) while Lake Michigan fish averaged 4.3 kg (9.5 lb), Chinook salmon (O. tshawytscha) have also been planted into U.S. waters since 1967 in numbers which reached 150,000 in 1970. Returns have been limited but growth appears to be good; at Age II the fish recaptured as jacks from the 1968 planting averaged 1.4 kg (3.1 lb), while the three-year-olds from the 1967 planting averaged 3.3 kg (7.2 lb).

It is convenient to regard immigrants to the lake through the canals at its outlet as inadvertent introductions. The most important of these, the sea lamprey (P. marinus) has already been discussed. The smelt (0. mordax) whose introduction has been documented by Van Oosten (1937b) are now ubiquitous and abundant in the lake as the commercial yields indicate, and may, as suggested earlier, be significant competitors of lake herring. The alewife (Alosa pseudoharengus (Wilson)), so significant as a competitor with the planktivorous coregonines of the other Great Lakes (Smith, 1968, 1972), has been present in the lake since at least 1953 but has not established abundant populations at least as yet. The carp (Cyprinus *carpio* Linnaeus) has long been established in small numbers in certain shallow bays along both sides of the lake. It is not abundant enough to be fished commercially. It is probable that all these fish entered the lake as adults or subadults and certain that the sea lamprey did so (Lawrie, 1970).

Still another inadvertent introduction was that of small (?) numbers of fingerling pink salmon (Oncorhynchus gorbuscha (Walbaum)) into Thunder Bay in the spring of 1956 (McKay, 1963). Following six generations which produced only scattered reports of small runs of stunted spawning adults in the odd years 1957 to 1967, the seventh and eighth generations have proven much more abundant and widespread. They have not been taken in the bottom set gill nets of the commercial fishery and this together with the small size at spawning, just over 0.5 kg (1 lb), points to their being pelagic and largely planktivorous. Presumably they should be added to the list of species which are potential competitors with the lake herring for food. If their population continues to expand the competition could be serious.

SUMMARY

A slim record, extending back almost four centuries, permits evaluation, albeit hardly rigorously, of the history of Lake Superior and its complex drainage basin. Exploitation of the forests, especially by the pioneering lumbering industry between 1860 and 1920, must have greatly accelerated the flow of both dissolved and particulate material to the lake. However, the denuded areas are now substantially reforested with second growth. Accordingly the situation has again stabilized so that available records of lake water chemistry provide only an equivocal hint of this upheaval. Because of the low level of present human activity the lake is neither significantly enriched from domestic or agricultural sources nor contaminated by industrial wastes, except locally. Hence it remains, as its morphometry, climate, and the nature of its drainage basin dictate, a highly oligotrophic lake with a flora and fauna to match.

Although the lake has not greatly changed from its pristine condition stocks of every fish species of commercial importance have clearly been severely depleted. Depreciation of the fluvial, estuarine, and shallow water benthic environment by the great quantities of woody allochthonous materials poured into them by the lumbering and pulp and paper industries in the past may have adversely affected fish stocks in the immediate areas concerned, especially those of lake sturgeon (Acipenser fulvescens) and lake whitefish *(Coregonus clupeaformis).* Recent declines, on the other hand, can, in many cases, be correlated with predation by sea lamprey *(Petromyzon marinus).* However, without exception, the histories of all species provide evidence suggestive of extensive overfishing long before sea lamprey entered the lake. That the depletion was not obvious sooner seems likely to have been owing to the sequential manner in which individual stocks were exploited and the fact that catch statistics for very large areas were pooled for publication and review, thus masking the process until well advanced. Recovery from these declines has been limited but measures to control sea lamprey coupled with modern hatchery technology clearly provide prospects for rejuvenating some existing stocks or developing entirely new ones.

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