SECTION 18

HISTORY OF CHANGES IN FISH SPECIES OF THE GREAT LAKES

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INTRODUCTION

Changes began in the fish-species complex in the Laurentian Great Lakes almost immediately after the first permanent settlers arrived in the basin in the early 1800's. Changes occurred slowly at first, but accelerated with the increased activities of man. These changes continue today and will continue in all probability for decades or even centuries because man's manipulations of the environment are continuing.

The Great Lakes are young; only about 10,000 years have passed since the melting of the glaciers. Youthful lakes such as these are generally characterized by low biological productivity, low nutrient content, and high transparency; they are often deep and cold. So are the Laurentian Great Lakes even today. With the exception of a few areas, the waters of the Great Lakes are of excellent quality and can be used as potable water without treatment. Yet man's impact on these lakes, especially on the fish populations, has been so drastic that the Laurentian Great Lakes have been used as worldwide symbols of accelerated aging. Some scientists have estimated that the lakes, especially Erie and Ontario, have aged more in the past 150 years than in the preceding 10,000 years. That changes of this magnitude could occur in lakes as large as the Great Lakes was not considered possible only a few years ago. Today, however, we are beginning to realize the tremendous capacity we possess to change (usually to our detriment) even the oceans and the atmosphere.

The purpose of this paper is to discuss the changes which have taken place in the fish populations of the Great Lakes and the stresses which have caused these changes. It has become obvious that many of the causes of the declines are the results of deliberate actions rather than subtle unpredictable factors.

The stresses which have been placed on the fish communities of the Great Lakes have been sequential and reflect the progress of man's occupation of the basin and his technological development. The most obvious and primary direct stress has been the intensive and selective exploitation of the fish stocks. This stress began early in the 19th century and continues to some degree today. Environmental stresses have not been as direct or as obvious, but were present as early as 1830 and have been additive as well as continuous. Environmental stress on the fish of the Great Lakes has been of five general types:

(1) Physical stress resulting from modification of the watershed by deforestation, blockage of tributaries, and drainage of marshes. This primarily affected anadromous species and began during the period of low human population density.

(2) Biological stress caused by the introduction and colonization of exotic species. Introduction of new species began before 1900 and continues today.

(3) Chemical stress (first phase) in the form of oxygen-consuming organic material dumped into tributaries and bays, and increased plant nutrients in the inshore areas.

(4) Chemical stress (second phase) caused by toxic chemicals such as chlorinated hydrocarbons and heavy metals.

(5) Thermal stress - more a future concern than a present concern.

The direct effects of the environmental changes on the fish populations are seldom observed and perhaps rarely occur. Indirect effects of these changes are often cited, but only occasionally quantified. In lakes as large as the Great Lakes, cause and effect are separated in time and distance to an extent that only after an event can the two be linked. This is the situation with the continuous change in the abundance of Great Lakes fish species.

We all recognize the fact that the stresses, be they exploitation, destruction of spawning grounds, oxygen depletion, increased water temperature, change in available food, or competition with introduced species, cannot often be isolated and analyzed separately. This paper is a summary of the changes that have occurred in the fish communities of the Laurentian Great Lakes from the early 19th century to the present. The changing composition of fish populations in the Great Lakes has been the subject in recent years of many articles in scientific and popular publications. The most exhaustive discussion of these changes occurred in a recent (1971) international symposium on "Salmonid Communities in Oligotrophic Lakes" (SCOL). These papers were published as a special issue of the Journal of Fisheries Research Board of Canada in 1972. This publication contains seven papers exclusively on the Great Lakes, including case histories of each of the five Laurentian Great Lakes: Superior, Huron, Michigan, Erie, and Ontario (Figure 1). Other comprehensive papers on changes in Great Lakes fish species are by Smith (1964, 1968) and Christie (1974).

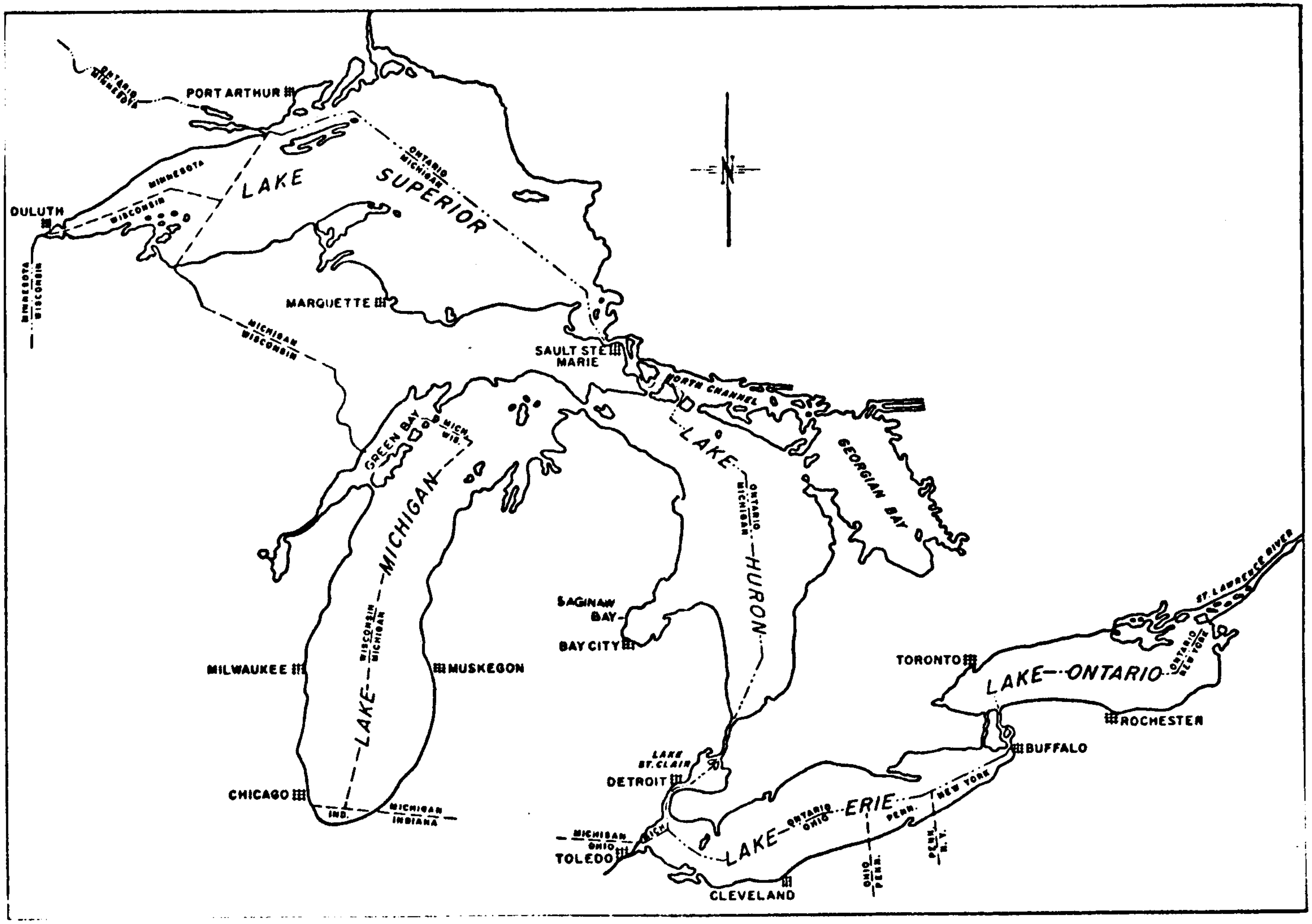

Figure 1. The St. Lawrence Great Lakes with interstate and international boundaries.

IN THE BEGINNING (TO 1850)

Fish Communities

The fish-species complex in the Great Lakes has changed drastically. Unlike many large lakes of the world, especially the large African lakes and Lake Baikal (USSR), the Laurentian Great Lakes have had only 10 thousand years between the retreat of the glaciers and the coming of man to produce, through evolutionary forces, a complex of species that is unique to the system.

The Great Lakes system did produce a few unique species in this short period, indicating that the processes were well underway to further species diversity. The evidence for this conclusion is best illustrated by the five endemic species (Smith, 1957; Scott and Crossman, 1973), all of the subfamily Coregoninae (whitefish) in the Samonidae (salmon family). These five species listed in descending order of size were:

deepwater cisco	-	*Coregonus johannae*
longjaw cisco	-	*Coregonus alpenae*
shortnose cisco	-	*Coregonus reighardi*
kiyi	-	*Coregonus kiyi*
bloater	-	*Coregonus hoyi*

According to Scott and Crossman (1973) all five species were found in Lakes Huron and Michigan, four in Lake Superior, three in Lake Ontario, and one in Lake Erie.

In addition to the five endemic species of ciscos, these wider ranging species were also present: lake herring (*Coregonus artedii*); blackfin cisco (*Coregonus nigripinnus*); and shortjaw cisco (*Coregonus zenithicus*). These eight species of ciscos, together with the lake whitefish (*Coregonus clupeaformis*) and round whitefish (*Coregonus cylindraceum*), characterized the Great Lakes fish community. Most of the species of the whitefish subfamily, especially the ciscos, were inhabitants of deep, cold water and therefore reached their greatest diversity in Lakes Superior, Huron, Michigan, and Ontario (Table 1). The dramatic alteration in the species complex of deepwater ciscos that subsequently occurred was documented by Smith (1964) for Lake Michigan.

In addition to the Coregonines other groups and species were abundant in the lakes. The dominant predators of the open waters present in all five lakes were the lake trout (*Salvelinus namaycush*) and burbot (*Lota lota*). In the bays and nearshore areas were: lake sturgeon (*Acipenser fulvescens*); northern pike (*Esox lucius*); suckers (primarily *Catastomus catastomus* and *C. commersoni*); channel catfish (*Ictalurus punctatus*); bullheads (*Ictalurus* spp.); white bass *Morone chrysops*; freshwater drum (*Aplodinotus grunniens*); and three species of the perch family: yellow perch (*Perca flavescens*); walleye (*Stizostedion vitreum*); and sauger (*Stizostedion canadense*). All of these species have been historically of commercial significance. The Atlanta salmon (*Salmo salar*) and American eel (*Anguilla rostrata*) were also abundant and became commercially important only in Lake Ontario.

TABLE 1. DIMENSIONS OF THE GREAT LAKES[a]

Lake	Length (miles)	Breadth (miles)	Water surface (miles)	Drainage basin (miles)	Average surface elevation above mean sea level since 1860 (ft)	Mean discharge (cfs)	Maximum depth (ft)	Mean depth (ft)
Superior	350	160	31,820	80,000	602.20	73,300	1,333	487
Michigan	307	118	22,400	67,860	580.54	55,000	923	276
Huron	206	183	23,010	72,620	580.54	177,900	750	195
St. Clair	26	24	490	7,430	574.88	178,000	21	10
Erie	241	57	9,930	32,490	572.34	195,800	210	58
Ontario	193	53	7,520	34,800	246.03	233,900	802	283

[a]From Beeton and Chandler, 1963.

Knowledge of the presence and relative abundance of the species listed thus far is based on records of the harvest of these species by commercial fishermen. Species not of great commercial value were, of course, also present in the lakes. A complete list of all species known to have been present in the lakes would be too long to include for the purposes of this paper. Our knowledge of changes in abundance of a few of these species, however, is sufficient to warrent their inclusion. An abundant forage species in the deeper water of all the lakes was the fourhorn sculpin (*Myoxocephalus quadricornis*). The slimy sculpin (*Cottus cognatus*) inhabited intermediate depths in all lakes. The inshore waters contained a variety of species of several families, especially the Cyprinidae. Among the more abundant species were the emerald shiner (*Notropis atherinoides*) and the spottail shiner (*Notropis hudsonius*).

Thus, when settlement began in the first half of the 19th century, the lakes were occupied by a supposedly stable community of fish species which inhabited all niches from the deepest waters of the subartic Lake Superior to the shallow bays and marshes of Lake Erie.

Environmental Conditions

Physiochemical conditions of the lakes were not measured before the end of the 19th century. Beeton and Edmondson (1972) used as a basis for evaluating the "natural" chemical condition the limited chemical data available about 1900 as indicative of the pristine quality of the lakes (Table 2).

TABLE 2. ESTIMATED AVERAGE CONCENTRATION OF DISSOLVED CHEMICAL CONSTITUENTS IN THE GREAT LAKES PRIOR TO 1900 (EXPRESSED IN MG/LITER)[a]

Lake	Total dissolved solids	Calcium	Sulphate	Chloride	Sodium and potassium
Superior	60	13	4	2	3
Michigan	128	34	5	2	-
Huron	108	24	6	4	4
Erie	142	31	13	7	7
Ontario	140	31	15	7	6

[a]From Beeton, 1969.

Based on these few constituents, Lakes Michigan, Erie, and Ontario were similar in chemical composition (Table 2). Lake Superior's chemical levels were substantially below all the others. Lake Huron receives approximately 41% of its inflow from Lake Superior, 31% from Lake Michigan, and 28% from the Lake Huron basin. Apparently the basin is a major contributor to the characteristics of the water quality, because the total dissolved solids are much higher than would be expected based only on a mixture of the waters from Lakes Superior and Michigan. The Lake Erie watershed apparently contributed significant amounts of calcium, sulphate, chlorides, and sodium-potassium to the waters flowing into Lake Ontario, because their chemical characteristics are nearly identical. Although differences between lakes were large compared to the range between other natural bodies of water, the five Great Lakes were remarkably similar.

Analysis of nutrient concentrations for the Great Lakes has been made only in recent years; therefore, base levels are only now being established. Estimates based on recent values for phosphorus and nitrogen indicate that the levels in the mid-1800's were less than 10 μg/liter for phosphorus and usually less than 1 mg/liter for total nitrogen in the three upper lakes (Superior, Huron, and Michigan). The Great Lakes in the 1900's would have been classified as oligotrophic (as defined by Hutchinson, 1957) with the probable exception of Lake Erie.

The order of the lakes, if listed from the greatest to the least fishery productive potential in the 1800's, probably would be Lake Erie, Lake Ontario, Lake Michigan, Lake Huron, and Lake Superior (Figure 2).

THE INITIAL IMPACT OF SETTLEMENT (1850-1900)

Changes in Fish Populations

The first environmental stresses on the Great Lakes ecosystem were primarily caused by physical alterations in the basin, particularly in the lower lakes. These alterations were deforestation of the watershed and siltation and blockage of streams. These changes mainly affected the tributaries and consequently the obligate anadromous species. Christie (1972) reported the Atlantic salmon had begun to decline as early as 1830 in Lake Ontario and was extinct, or nearly so, by 1900. Documentation of the early proliferation of mills and dams was given by Christie (1972) based on data from Richardson (1944). On the Ganaraska watershed (one of the larger Canadian rivers tributary to Lake Ontario) at least two sawmills, two grist mills, and two dams had been constructed by 1800. Construction of the mills and dams increased rapidly, reaching a maximum of 34 sawmills, 19 grist mills, 4 woolen mills, and 34 dams by 1860. In 1930, 15 dams still remained on this single tributary. Christie (1972) considered the elimination of the Lake Ontario Atlantic salmon stock as the best known example of the effects of despoilation on a species habitat.

The lake sturgeon population in all the lakes was greatly reduced during this period. Prior to 1903 the annual commercial production fluctuated between 100,000 pounds and 500,000 pounds in Lake Ontario (Baldwin and

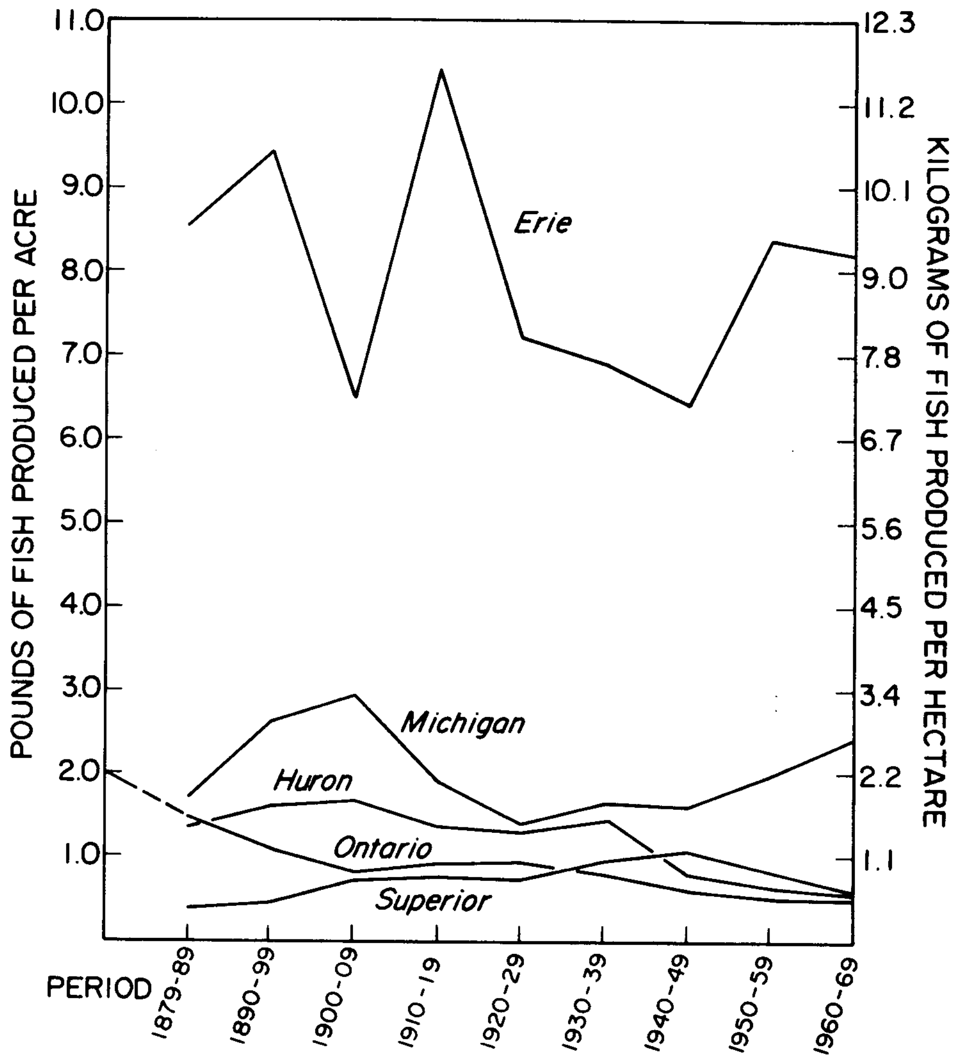

Figure 2. Average number of pounds and kilograms of fish produced per acre and hectare by the commercial fishery of the Great Lakes for 10-year intervals (data from Smith 1972).

Saalfeld, 1962). After 1910 production never exceeded 25,000 pounds and averaged near 15,000 pounds for many years. In Lake Erie production dropped from 1 - 5 million pounds in the late 1800's to less than 10,000 pounds after 1910 (Baldwin and Saalfeld, 1962). Similar magnitudes of decline occurred during the same period in Lake Huron, Michigan, and Superior. The cause-and-effect relationship apparent between watershed and stream modification and Atlantic salmon extinction was not as direct with the sturgeon. The environmental requirements of the sturgeon were not as narrow as those of the Atlantic salmon; however, the slow growth rate and late maturity of the sturgeon were also factors in this species, inability to recover from even low exploitation rates.

Christie (1972) also lists the blackfin cisco (*Coregonus nigripinnus*) as a species that became either extinct or greatly reduced in Lake Ontario before 1900. Wells and McLain (1972) infer a sharp decline in the abundance of this species in Lake Michigan in the early 1900's. The blackfin was considered commercially extinct in Lake Superior by 1910 (Lawrie and Rahrer, 1972). This species of cisco inhabited the deep, open waters of the lakes; consequently, environmental modification of the tributary and watershed was not a factor in their decline. This species was the largest of the ciscos, and selective exploitation for it was the probable cause of its decline (Wells and McLain, 1972).

The lake trout population in Lake Erie was also decimated during this period. Hartman (1972), in discussing this species in Lake Erie, states: "Perhaps the decline of the lake trout population to near extinction best illustrates the effect of essentially one stress: intensive exploitation." Apparently, environmental stress was not a factor in the decline of lake-dwelling species during the 1800's.

In addition to the effective loss of at least one species during the 1800's, several new species became abundant. Christie (1972) listed the following species as becoming established in Lake Ontario before 1900: alewife (*Alosa pseudoharengus*); gizzard shad (*Dorosoma cepedianum*); brown trout (*Salmo trutta*); carp (*Cyprinus carpio*); and the goldfish (*Carassius auratus*). Some of these species were also introduced to the other lakes during this period. There was a flourishing fishery for carp in Lake Erie by 1899, when over 3.5 million pounds were landed (Baldwin and Saalfeld, 1962).

Environmental Changes (Age of Physical Alterations)

Man's effect on the Great Lakes ecosystem in the last half of the 19th century was dramatic and permanent. He removed the forest, built dams, constructed mills, directly exploited the fish, and opened new and more direct passage between the ocean and the lakes, as well as between Lake Ontario and the upper lakes (Figure 3).

The effects of these physical modifications of the environment ranged from immediate (Atlantic salmon extinction) to long-term (invasion of marine species). The Erie Canal, which provided a connection between the Atlantic Ocean and Lake Ontario, was opened in 1819 and extended to Lake Erie in

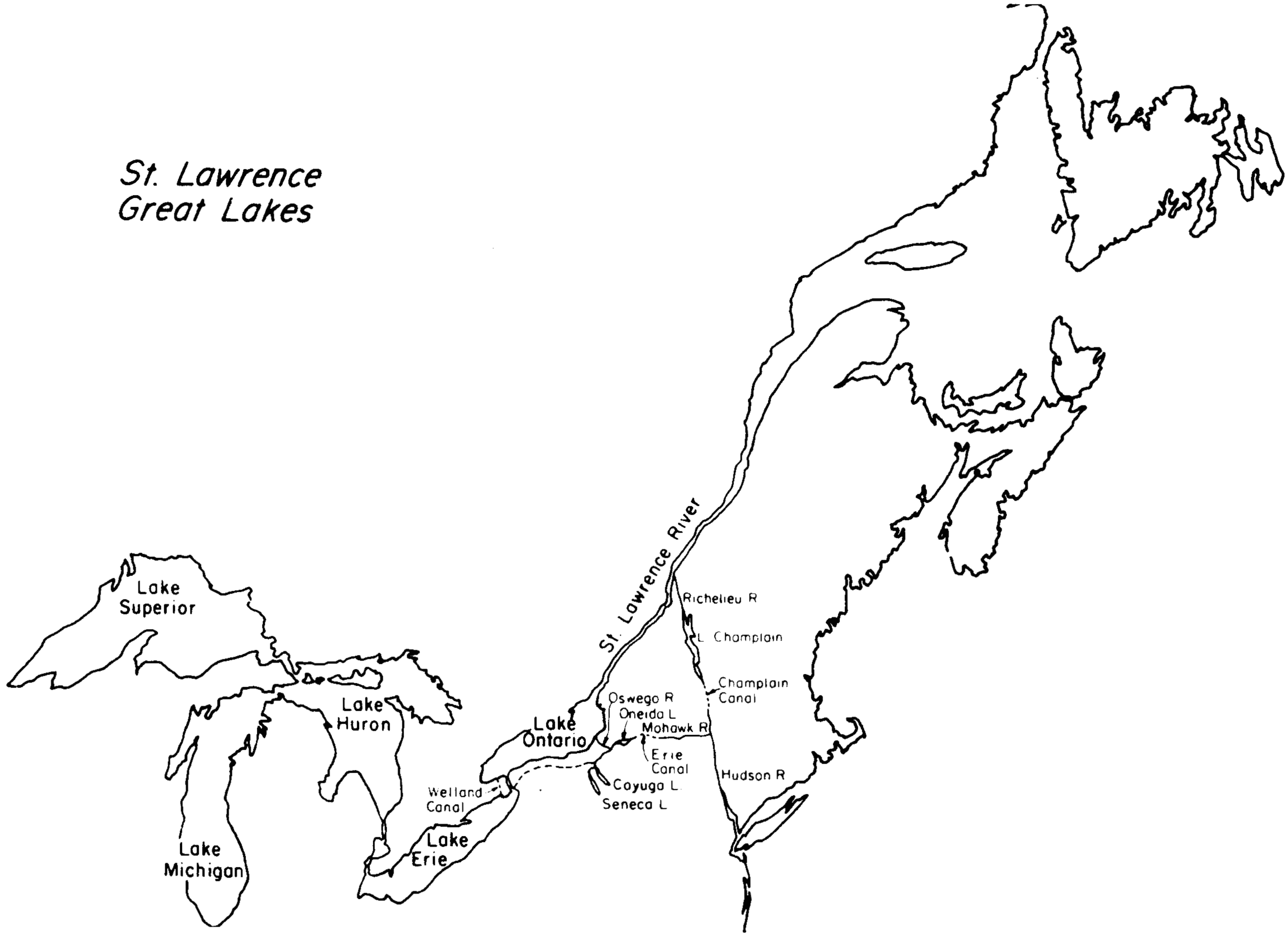

Figure 3. The St. Lawrence Great Lakes showing canals between central Atlantic Ocean and the lakes.

1825. The Welland Canal, which was opened in 1829, connected Lake Ontario to the upper lakes. Previously the passage of fish between Lakes Ontario and Erie was blocked by Niagara Falls. Although no biological changes were noticed for many years after the opening of the canals, the stage was set for dramatic and catastrophic changes to occur decades later (Aron and Smith, 1971).

The chemical characteristics of the open waters of the lakes were assumed to be essentially the same at the end of the 19th century as at the beginning (Beeton and Edmondson, 1972). Although the settlement of the Great Lakes basin had advanced rapidly in the 19th century, from a population of a few thousand early in the century to over 10 million in 1900 (Table 3), the effects on water quality in the lakes were yet to be felt.

By 1900 man, in less than 100 years, had placed the following stresses on the biological communities of the Great Lakes: siltation of streams; blockage of tributaries; increase in stream temperatures; and establishment of exotic species. In addition, he had removed barriers to migration between the lakes; had established fisheries capable of overexploitation of most species in all the lakes; and had begun using the lakes as the receiver of man's domestic and industrial waste.

TABLE 3. ESTIMATED POPULATION (MILLIONS) IN GREAT LAKES BASIN - 1900-1960[a]

Lake basin	1900	1925	1950	1960
Superior	0.4 (50)[b]	0.6 (33)	0.8 (12)	0.9
Michigan	4.0 (-20)	3.2 (50)	4.8 (23)	5.9
Huron	1.0 (20)	1.2 (25)	1.5 (33)	2.0
Erie	3.0 (93)	5.8 (48)	8.6 (17)	10.1
Ontario	2.0 (25)	2.5 (20)	3.0 (33)	4.0
Total	10.4 (28)	13.3 (41)	18.7 (22)	22.9

[a]From Beeton, 1969.

[b]Numbers in parentheses indicate percentage change in the ensuing time interval.

ENRICHMENT AND INVASION (1900-1950)

The stage was set and the signs were present in 1900 for what was to follow. Changes in the biological, chemical, and physical environment of the Great Lakes became the rule and not the exception. The records of these changes, unfortunately, are incomplete, often inaccurate, and, for the fish populations, often not a true representation of species abundance. The analysis of changes in the abundance of species until recently was based on the reported catch of commercial fishermen. High prices often maintained high catches in the face of a decreasing abundance. Conversely, low production often was due to low prices and lack of demand for a species rather than low population levels. Despite these handicaps, the changing conditions often became too obvious to be ignored.

Changes in fish-species composition, losses and gains, differ in time between the lakes, but the sequence of species change often was similar (Smith, unpublished manuscript). In general, the species that declined were those most sought after by the commercial fishery. A few significant exceptions exist to this generalization, and it is the exceptions which clearly indicate stresses other than fishing on the biological communities of the Great Lakes.

Changes which occurred in native fish species of commercial interest between 1900 and 1971 are summarized in Table 4. Detailed discussion of these declines by species and lakes appear in Smith (1968), the papers of the SCOL Symposium (1972), and Christie (1974). The data presented in Table 4 refer to production trends in the total lake and, therefore, are not descriptive of events in the unique ecological areas of each lake such as the Bay of Quinte in Lake Ontario, the western basin of Lake Erie, Saginaw Bay of Lake Huron, or Green Bay of Lake Michigan (Figure 1). These geographic areas were, and are, more shallow and productive and warmer than the open portions of the lake to which they are connected. The fish-species complex here was also more diverse than in the open lake, containing many warmwater species, especially the centrarchids and percids.

Ecological and Cultural Changes, 1900-1925

During the first quarter of the 20th century, the northern pike fishery was reduced to a fraction of former production; lake whitefish in Lake Ontario and lake herring in Lake Erie began declining; the first sea lamprey was reported in Lake Erie; and the first rainbow smelt were found in Lakes Michigan and Huron. The gains and losses in these and other species were to be repeated many times in the next 50 years in the other lakes.

The introduction of the smelt into Crystal Lake in the drainage basin of Lake Michigan was deliberate, but its establishment in Lake Michigan was not contemplated, nor was its rapid spread to other Great Lakes. The sea lamprey reached Lake Erie nearly 100 years after the Welland Canal was opened and established itself in the upper lakes. The beginning of the declines in lake whitefish and lake herring were, of course, undetected at the time and thus alarmed no one.

TABLE 4. SUMMARY OF FISH SPECIES DECLINE IN THE GREAT LAKES BY YEAR, LAKE, AND CURRENT COMMERCIAL PRODUCTION

Species and lake	Beginning of decline (year)	Product first below 100,000 pounds (year)	1974 production (1,000's pounds)	Potential for recovery (H,M,L)[a] and reason
Lake trout				
Ontario	1928	1942	1	H - stocking and sea lamprey control (s.l.c.)
Erie	?	1900	0	L - environmental
Huron[b]	1935	1945	1	H - stocking & s.l.c.
Michigan	1943	1950	37	H - stocking & s.l.c.
Superior	1950	c	526	H - stocking & s.l.c.
Lake whitefish				
Ontario	1924	1966	16	L - environmental
Erie	1953	1960	1	L - environmental
Cisco (chubs)				
Ontario	1941	1950	0	L - environmental
Huron[b]	1961	1970	50	L - environmental
Michigan	1970	c	3,267	L - environmental
Superior	1965	c	1,926	L - environmental
Lake herring				
Ontario	1941	1953	32	L - environmental
Erie	1924	1958	0	L - environmental
Huron[b]	1939	1957	2	L - environmental
Michigan	1952	1963	6	L - environmental
Superior	1961	c	2,186	M - stocking
Northern pike				
Ontario	1933	1938	21	L - environmental
Erie	1914	1924	15	L - environmental
Burbot				
Ontario	1930[d]	1934[e]	0	L - environmental
Erie	1947[d]	1961[e]	0	L - environmental
Michigan	1948[d]	1959	230[f]	H - s.l.c.
Blue pike				
Ontario	1952	1955	0	L - environmental
Erie	1955	1959	0	L - environmental
Sauger				
Erie	1945	1955[e]	0	M - stocking
Huron	1935	1937[e]	0	L - environmental

[a]H, M, and L indicate high, medium, and low potential for recovery, respectively.

[b]Excludes Georgian Bay and North Channel.

[c]Remains above 100,000 pounds.

[d]Production normally less than 100,000 pounds.

[e]Production less than 10,000 pounds.

[f]First exceeded 100,000 pounds in 1973.

Environmental changes, except in streams and bays near centers of high human population density, were nearly undetectable in 1925 in the lakes proper. Changes had occurred, however, in Lakes Michigan, Erie, and Ontario in the few chemical constituents for which data are available (Table 5). The absolute concentrations of these constituents, even the highest levels, were well below levels of ecological or toxicological concern. The rates of change, especially in total dissolved solids, sulphur, and chloride, however, are staggering considering the tremendous volume of water which had been changed as much as 160% in only 25 years.

TABLE 5. ESTIMATED AVERAGE CONCENTRATION OF DISSOLVED CHEMICAL CONSTITUENTS IN THE GREAT LAKES IN 1925 (EXPRESSED IN MG/LITER)[a] WITH PERCENTAGE CHANGE AFTER 1900 IN PARENTHESES

Lake	Total dissolved solids	Calcium	Sulphate	Chloride	Sodium and potassium
Superior	58 (-3)	13 (0)	4 (0)	2 (0)	3 (0)
Michigan	143 (+12)	34 (0)	13 (+160)	4 (+100)	-
Huron	108 (0)	24 (0)	9 (+50)	4 (0)	4 (0)
Erie	146 (+3)	33 (+6)	16 (+23)	11 (57)	7 (0)
Ontario	149 (+6)	34 (+10)	18 (+20)	11 (57)	7 (17)

[a]From Beeton, 1969.

The increase in population growth in the basins of the Great Lakes was approximately 28% between 1900 and 1925 (Table 3). Growth in numbers was greatest in the basins of Lakes Erie and Ontario. The population in the Erie basin increased 93% to 5.8 million, and in the Lake Ontario basin the increase was 25% to 2.5 million. Lake Michigan's basin effectively lost 0.8 million when the Chicago Sanitary Canal, which diverted the waste from the city to the Mississippi River drainage, was completed in 1900. The increasing urbanization and industrial expansion was the probable cause of the increase in the chemically conservative ions. Undoubtedly, concentrations of other chemical components also increased, especially the plant nutrients phosphorus and nitrogen. The load of oxygen-demanding organic compounds can also be assumed to have increased.

The stresses causing the decreases in some native fish species in the lower lakes by 1925 were man caused, principally by heavy exploitation. The role of environmental change, especially water-chemistry change, in reduction in fish populations apparently was minor except in the tributaries and bays. The drainage of marshes, however, may have been a significant factor in the loss of the northern pike as an important commercial species in Lake Erie. The establishment of the two marine species, smelt and lamprey, was too recent to have had a measurable impact on other fish species by 1925.

Environmental and Cultural Changes, 1925-1950

Several catastrophic events affecting the Great Lakes fish stocks occurred during this period. The most damaging event was the invasion by the parasitic sea lamprey of all the upper Great Lakes. After at least 50 years in Lake Ontario, the lamprey made its way into Lake Erie in 1923 where it did not flourish because of the lack of suitable spawning streams and limited deepwater environment. In 1932 the first sea lamprey was reported in Lake Huron; 4 years later the lamprey was in Lake Michigan; and by 1946 the first report was made of a sea lamprey in Lake Superior (Table 6). Three years after the first sea lamprey was reported in Lake Huron, the production of lake trout started to decline (1935), and by 1946 (Table 4) the commercial fishery for this species in Lake Huron proper was finished, although the fishery in Georgian Bay lasted another 9 years. Lake trout production began to decline in Lake Michigan in 1943 (7 years after the first lamprey was reported); by 1950 production dropped below 0.1 million pounds (Table 4), and the species was virtually extinct 3 years later. Only 18 years passed from the time the first sea lamprey was reported in Lake Huron (1932) until the species was commercially extinct in Lakes Huron and Michigan.

The demise of the lake trout population in Lake Ontario and the role of the sea lamprey is more complicated than in the upper lakes. Whether the sea lamprey was endemic to Lake Ontario (Christie, 1972), or became established after the opening of the Erie Canal (Smith, 1974), at least 75 years passed before the lake trout production began its final decline (1928). A substantial fishery continued, however, for another 10-12 years. The species was last reported in the commercial catch statistics as late as 1964 (Baldwin and Saalfeld, 1962, with supplement). That the sea lamprey was a strong factor in the loss of lake trout in Lake Ontario is undisputed; the reasons why the struggle lasted so long remain a subject of speculation.

The sea lamprey's favored prey was the lake trout, but other species as well were victims of this marine invader. Larger individuals of lake whitefish, ciscos, lake herring, suckers, and burbot were attacked by the sea lamprey. The production of burbot (never a prime commercial species) began to decline in Lake Ontario in 1930, in Lake Erie in 1947, and in Lakes Huron and Michigan by 1948 (Table 4). The burbot population became commercially extinct in these lakes about 1960.

Other species also began declining during this period, although the declines were not related to the sea lamprey. The sauger began declining in Lake Huron (primarily Saginaw Bay) in 1935; 2 years later the species was commercially extinct. Beeton (1969) gave the reason for the decline as the development of an environment not suitable for the sauger or the Saginaw

TABLE 6. FISH-SPECIES INTRODUCTIONS IN THE GREAT LAKES BY YEAR AND LAKE, FIRST YEAR OF COMMERCIAL SIGNIFICANCE, AND CURRENT PRODUCTION

Species	First recorded		First reported in commercial catch		Reached commercial significance[a]		1974 Production	
	Year	Lake	Year	Lake	Year	Lake	1,000 pounds	lake
Sea lamprey[b]	1800's	Ontario						
	1921	Huron						
	1936	Michigan						
	1946	Superior						
Alewife[b]	1873	Ontario	?		1920's	Ontario	1,332	Erie
	1931	Erie	?					
	1933	Huron	?					
	1949	Michigan	1956	Michigan	1957	Michigan	45,508	Michigan
	1953	Superior						
Gizzard shad	1900	Ontario						
Coho salmon	1968	Ontario						
	1968	Erie						
	1967	Huron						
	1966	Michigan						
	1966	Superior						
Chinook salmon	1969	Ontario						
	1970	Erie						
	1967	Huron						
	1967	Michigan						
	1967	Superior						
Rainbow smelt[b]	1923	Michigan	1946	Ontario	1952	Ontario	110	Ontario
	1925	Huron	1946	Erie	1952	Erie	15,766	Erie
	1930	Superior	1935	Huron	1950	Huron	215	Huron
	1931	Ontario	1931	Ontario	1933	Michigan	1,748	Michigan
	1935	Erie	1935	Superior	1956	Superior	2,853	Superior
Carp	1885-1895	Ontario	1899	Ontario	1910	Ontario	411	Ontario
	1880-1895	Erie	1892	Erie	1893	Erie	3,152	Erie
	1880's	Huron	1899	Huron	1908	Huron	739	Huron
	1880's	Michigan	1893	Michigan	1903	Michigan	3,244	Michigan
	?	Superior						
Goldfish	?		1929	Erie	1933	Erie	54	Erie
White perch	1950[c]	Ontario	1955	Ontario	1964	Ontario	371	Ontario

[a]Production exceeded 100,000 pounds.
[b]Year of record from Smith, 1972.
[c]Year of record from Christie, 1972.

TABLE 7. FISH-SPECIES IN THE GREAT LAKES THAT HAVE EXPERIENCED SEVERE DECLINES, LAKE AFFECTED, AND SUSPECTED CAUSE OF DECLINE

Species	Principal lakes affected	Primary cause(s) of decline
Atlantic salmon	Ontario	Deterioration and blockage of streams, exploitation
Sturgeon	All lakes	Exploitation, destruction of spawning streams
Lake trout	Erie	Exploitation
Northern pike	Erie, Ontario Huron	Destruction of spawning areas, exploitation
Lake herring	All lakes	Exploitation, environmental changes, competition with introduced species
Burbot	All lakes	Sea lamprey, environmental change
Cisco (chubs)	All lakes	Exploitation, competition with introduced species, sea lamprey
Sauger	Huron, Erie	Environmental change, exploitation
Lake trout	All lakes (except Erie)	Sea lamprey, exploitation
Walleye	All lakes	Environmental changes, exploitation, destruction of spawning streams
Blue pike	Erie and Ontario	Environmental changes, exploitation
Whitefish	All lakes	Environmental changes, exploitation, sea lamprey
Yellow perch	Erie, Huron, Michigan	Competition with introduced species, exploitation, environmental changes
Fourhorn sculpin	Ontario, Erie	Competition with introduced species, environmental change
Emerald shiner	Michigan	Competition with introduced species, environmental change

Bay populations of walleye and whitefish. In Lake Erie the sauger production fell below 0.5 million pounds in 1946 (Baldwin and Saalfeld, 1962) for the first time after nearly 70 years of production between 1 and 6 million pounds. Environmental changes, plus heavy exploitation, were believed to be the causes (Table 7).

The decline of the lake herring, historically the most productive species in the Great Lakes (Smith, 1968), began in Lake Erie in 1925, and by 1963 this fish had become commercially extinct in all the lakes except Superior. Heavy exploitation was undoubtedly a factor in the decline of the lake herring. The role and impact on this decline of introduced alewife and smelt and of environmental factors, however, have not been isolated. The collapse of the lake herring stocks in the mid-1920's was the event most responsible for stimulating interest and concern in the welfare of the Great Lakes aquatic environment. This concern was primarily responsible for identifying the rapid deterioration in the water quality of Lake Erie, which is discussed in a following section.

Water Quality and Population Changes, 1925-1950

Changes in dissolved chemical constituents continued to accelerate after 1925 in all the lakes except Superior (Table 8). The absolute values of these "indicator" chemical parameters are of no toxicological concern, but again the rate of change indicated substantial inputs from cultural and industrial sources. Concentrations of these and other chemical compounds must have been substantial in the receiving waters near the pollution source. The loss of whitefish, lake herring, sauger, and other species from the inner portions of Saginaw and Green Bays due to water quality changes would be expected.

TABLE 8. ESTIMATED AVERAGE CONCENTRATIONS OF DISSOLVED CHEMICAL CONSTITUENTS IN THE GREAT LAKES (EXPRESSED IN MG/LITER)[a] 1950 WITH PERCENTAGE CHANGE SINCE 1925 IN PARENTHESES

Lake	Total dissolved solids	Calcium	Sulphate	Chloride	Sodium and potassium
Superior	56 (-3)	13 (0)	4 (0)	2 (0)	3 (0)
Michigan	150 (5)	34 (0)	17 (31)	5 (25)	-
Huron	110 (2)	24 (0)	13 (44)	6 (50)	4 (0)
Erie	170 (16)	38 (15)	23 (44)	19 (73)	9 (29)
Ontario	172 (15)	38 (12)	25 (39)	19 (73)	10 (43)

[a]From Beeton, 1969.

Population Increases, 1925-1950

The population in the Great Lakes basin had exceeded 18 million by 1950 (Beeton, 1969), an increase of approximately 40% in 25 years (Table 3). Again, the greatest numerical growth was in the Lake Erie basin with an increase from 5.8 to 8.6 million (48%). The population in Lake Erie's basin was 46% of the total population and, combined with the Lake Ontario population, accounted for 62% of the total. The population in the Lake Michigan basin was nearly 5 million in 1950. This continued concentration of people in Michigan, Erie, and Ontario lake basins, with the associated municipal, industrial, and agricultural wastes, was the primary cause of the accelerated rate of increases in dissolved chemical constituents in these lakes.

Lake Erie--Demise is Heralded

The sudden collapse of the Lake Erie lake herring fishery in 1925 awakened the public to the need for scientific investigations into the causes of the precipitous decline. The magnitude of the decline in lake herring production was from an average of 26 million pounds per year in the previous decade to 6 million pounds in 1925, to less than a million pounds in 1929.

Since environmental factors were thought to be the cause of the lake herring decline, two intensive limnological studies (Wright, 1955; Fish, 1960) were initiated in 1928. Wright (1955) found unfavorable conditions in rivers and estuaries, but concluded that environmental changes in the open waters of the western basin of Lake Erie in 1928-30 had no adverse effect on the decline of fish stocks. Fish et al. (1960) also found no environmental basis for the decline of lake herring in the central and eastern basins in 1928-30. Although neither investigator found measurable environmental degradation in the open lake, their studies for the first time established a scientific base line of data on benthic organisms, plankton, and dissolved oxygen. The base line has subsequently been invaluable in measuring environmental changes in Lake Erie.

The effects of the sea lamprey on the lake trout stocks (previously discussed) were recognized in the 1940's, and attempts to control the lamprey began in 1946. Another decade passed, however, before an organized and substantial program was developed to control this destructive parasite.

CHANGE AND REHABILITATION (1950-1975)

Fish Stocks

Changes in abundance of fish stocks are continuing in 1975; however, many changes are now deliberate and controlled. Uncontrollable changes in native species (usually decreasing in numbers) and in introduced species (usually increasing in numbers) frequently occurred during the past 25 years.

1950's

Lake trout production reached zero in Lake Michigan and began to decline in Lake Superior in 1950. Walleye production started to decline in 1950 in Lake Michigan. Cisco (chub) production dropped below 100,000 pounds in Lake Ontario, the first of the lakes to lose its chub population.

In 1952 production of lake herring in Lake Michigan and blue pike in Lake Ontario began their "terminal" decline. Lake whitefish, blue pike, and walleye production began declining in Lake Erie by 1956. By 1959 production had fallen below 100,000 pounds for lake herring in Lake Ontario, Huron, and Erie; sauger in Lake Erie; and blue pike in Lakes Ontario and Erie. Within a few years the blue pike had become virtually extinct in Lakes Ontario and Erie. The emerald shiner, once exceedingly abundant, became extremely scarce in Lakes Michigan and Huron.

Increases also occurred in the 1950's. Smelt production exceeded 200,000 pounds in Lakes Ontario and Huron; 800,000 pounds in Lake Superior; 6 million pounds in Lake Erie; and 9 million pounds in Lake Michigan. The rainbow smelt had become a significant species in the commercial catch of all the lakes in less than 30 years after its introduction in Lake Michigan.

The first alewife was reported in Lake Michigan in 1949, and the species was first reported in the commercial catch in Lake Michigan in 1956. By 1957 production exceeded 100,000 pounds, and by 1958 (9 years after it was first reported) over 1 million pounds of alewives were produced in Lake Michigan. Similar rapid colonization of the white perch occurred in Lake Ontario; only 5 years elapsed between the first record of its presence (1950) and the first report of it in the commercial catch (1955).

1960's

During this decade species of the whitefish family continued to decline in the Great Lakes. Lake whitefish production fell below 100,000 pounds in Lakes Ontario and Erie; lake herring began declining in Lake Superior and fell below 100,000 pounds in Lake Michigan; deepwater cisco (chub) production began declining in Lakes Huron and Superior. Shallow water species also declined: walleyes in Lakes Michigan and Ontario; yellow perch in Lake Michigan; and northern pike in Lake Huron. The fourhorn sculpin, once abundant in Lake Ontario, was extremely rare in the 1960's. A major decline of the fourhorn sculpin during this period was also noted in Lake Michigan (Wells and McLain, 1972).

Rehabilitation of the Fish Stocks

Biologists recognized that rehabilitation of fish stocks, principally lake trout, could not begin until the sea lamprey was brought under control. A special agency, the Great Lakes Fishery Commission, was created in 1956 by a treaty between Canada and the United States to fund and coordinate existing efforts to control the sea lamprey. Initial control methods attempted to block spawning migrations into streams by means of mechanical and electrical barriers. This method proved ineffective. In 1957, after several years of research and testing thousands of chemicals, one was found which was toxic to the lamprey but not lethal to other fish. Treatment of lamprey-infested streams with the chemical 3-trifluoromethyl-4-nitrophenol (TFM) began in 1958. By 1962, 2 years after all known lamprey nursery streams had been treated in Lake Superior, success was verified when the number of adult lampreys at assessment barriers was reduced nearly 85% (Baldwin, 1964). The incidence of lamprey wounds on lake trout dropped sharply, and survival of lake trout increased dramatically in Lake Superior. A method of control had been found just in time to save the last natural population of lake trout in the Great Lakes. The first complete treatment of all Lake Michigan lamprey-infested streams was completed in 1963, Lake Huron in 1970, and Lake Ontario in 1972. Chemical treatment of streams at intervals of 2-4 years must continue, however, if the rehabilitation of lake trout and other species is to become permanent.

The introduction of Pacific salmon in the Great Lakes had been attempted many times, but had produced limited results until the successful introduction of the coho salmon (*Oncorhynchus kisutch*) in Lake Michigan in 1966. By 1969 coho and chinook salmon (*Oncorhynchus tshawytscha*) had been introduced into all the upper lakes. The purpose of stocking coho and chinook salmon in the Great Lakes was to increase the sport fishing potential and not to establish self-sustaining populations. "Successful" introduction, therefore, relates to rapid growth and high survival rates. The pink salmon (*Oncorhynchus gorbuscha*), however, was an "unplanned" plant in Lake Superior, where it succeeded in establishing spawning runs in 1959 and by 1975 had become established in Lakes Huron and Michigan.

Supplemental plantings of lake trout, following lamprey control, have been made since 1958 in Lake Superior. The stocks have been built up to near pre-lamprey levels. Reproduction of hatchery-reared fish has been disappointing, however. Only in the last 2 or 3 years has the outlook improved, when increasing numbers of young native trout have been reported.

The reintroduction of lake trout in Lake Michigan, beginning in 1965, has proved extremely successful in terms of survival and growth. No evidence of reproduction, however, has been reported. Lake trout are now being stocked in Lakes Huron and Ontario. Biologists continue to be optimistic about the reestablishment of self-sustaining populations of lake trout in all the Great Lakes, except Erie.

Salmonids other than lake trout and Pacific salmon have been stocked in the Great Lakes since the lamprey has been controlled. Steelhead trout (rainbow trout), brown trout, brook trout, and Atlantic salmon are now stocked in the lakes. Over 20 million salmonids annually are stocked in the Great Lakes. In 1974 the first experimental plant of hatchery-reared saugers was stocked in Lake Erie.

Environmental Changes, 1950-1975

Scientific investigations of environmental conditions of the Great Lakes have increased exponentially during the past 25 years. Changes in fish populations, benthic organisms, plankton, and water quality are now measured with greatly improved accuracy and frequency. The ability to control environmental conditions and to understand ecological interactions, however, remains a goal of the future.

Chemical changes--The increase in major ions continued in all the lakes except Superior during the last 25 years. The rates of increase in all the ions except calcium remain high for Lakes Ontario and Erie (Table 9). Population increases also were substantial in the basins of Lakes Ontario and Erie (Table 3) and probably account for the chemical changes.

TABLE 9. ESTIMATED AVERAGE CONCENTRATIONS OF DISSOLVED CHEMICAL CONSTITUENTS IN THE GREAT LAKES IN 1970 (EXPRESSED IN MG/LITER)[a] WITH PERCENTAGE CHANGE SINCE 1950 IN PARENTHESES

Lake	Total dissolved solids	Calcium	Sulphate	Chloride	Sodium and potassium
Superior	55 (-2)	13 (0)	4 (0)	2 (0)	2 (-33)
Michigan	155 (3)	34 (0)	20 (43)	7 (40)	5 (0)
Huron	115 (3)	27 (12)	17 (31)	7 (17)	4 (0)
Erie	206 (21)	38 (0)	27 (17)	27 (42)	14 (56)
Ontario	210 (22)	40 (5)	30 (20)	29 (53)	15 (50)

[a]From Weiler and Chawla, 1969.

Critically low dissolved oxygen (DO) concentrations had not been reported in the open waters of the Great Lakes until 1953. In that year Britt (1955) measured DO concentrations less than 1 mg/liter in the western basin of Lake Erie. Although the low DO levels lasted only a few days, it caused a substantial mortality in the burrowing mayfly (Hexagenia) population. In some areas of the western basin the entire population was killed, where more than 1,000 mayfly nymphs per square meter had previously been found (Britt, 1955). The first extensive zone of low DO (less than 1 ppm) was measured in 1959, in the western portion of the central basin of Lake Erie. An interagency synoptic survey of this basin in 1959 found an area of approximately 1,400 square miles which contained less than 1 ppm of DO in the hypolimnion. These conditions of low DO undoubtedly had occurred before 1959 (Carr, 1962).

Dissolved oxygen levels of less than 1 mg/liter occur annually in the bottom waters of the central basin of Lake Erie and by 1974 covered several thousand square miles. Oxygen depletion also has been reported in southern

Green Bay (Lake Michigan) and the Bay of Quinte (Lake Ontario). Low DO levels in the open waters of the other lakes have not been reported. The virtual extinction of the sauger and blue pike and the decline of the walleye population in Lake Erie are thought to be partially caused by the low DO conditions (Smith, 1974).

Toxic Substances in Fish

Chemical contaminants in Great Lakes fish have been measured with increasing frequency in the past decade (1965-75). Measurements were first made in 1965 of the residues of the insecticides DDT and dieldrin in Great Lakes fish. All 28 species for which DDT and dieldrin analysis has been made contained measurable levels. Several species (chubs, lake trout, lake herring) from Lake Michigan exceeded the U.S. Food and Drug Administration's (FDA) tolerance level of 5 μg/g in fish used for human consumption (Reinert, 1970). Since the use of DDT was banned in 1972, the level in Lake Michigan fish has decreased rapidly, from an average of 10 μg/g in bloater chubs before 1972 to less than 3 μg/g in 1974.

During the same period in which DDT levels were decreasing in Great Lakes fish, polychlorinated biphenol (PCB) levels were increasing. Again, the species containing the highest levels were lake trout and bloater chubs in Lake Michigan. The average concentration of PCB in Lake Michigan lake trout above 24 inches exceeded 20 μg/g in 1974. Concentrations above the FDA's 5 μg/g tolerance level have been reported in fish from Lake Ontario and Lake Huron, as well as Lake Michigan.

In 1969 mercury levels in excess of the FDA's tolerance level of 0.5 μg/g were discovered in several species of fish (including walleye and white bass) from Lakes St. Clair and Erie. Mercury levels above 0.5 μg/g were also reported from Lakes Superior and Ontario. Two years following curtailment of the source of mercury pollution to Lake St. Clair, the levels in fish began to decrease. In two instances (DDT and mercury) stopping the sources of chemical contaminants resulted in the rapid decline of the toxicants in the environment. This success should give support to continued efforts to solve problems by eliminating the direct cause.

The contamination of Great Lakes fish with levels of DDT, PCB, and mercury exceeding the FDA tolerance level has resulted in great financial hardship to the commercial fishing industry. Direct or even indirect adverse effects on the fish populations of the Great Lakes have not been detected. Apparently, DDT and PCB in the low nannogram-per-liter levels in the open lake waters have, through biomagnification, reached the microgram-per-gram level in fish tissue.

Changes in Benthos and Plankton

Changes in bottom-dwelling organisms have been documented by several investigators within the past 20 years: Britt (1955) and Carr and Hiltunen (1965) for Lake Erie; Schneider, Hooper, and Beeton (1969) for Saginaw Bay; Hiltunen (1967) for Lake Michigan. In all of these studies the changes have been from the more "pollution-intolerant" organisms (mayflies, caddisflies, amphipods) to "pollution-tolerant" forms (primarily oligochaetes and midge larvae) and from greater to lesser species diversity. The geographic areas affected by loss of intolerant organisms are being extended further into the lakes from the pollution sources (primarily river mouths). The effects of these changes on fish populations will remain speculative until the interactions can be quantitatively assessed.

Phytoplankton and zooplankton populations have also changed markedly in many areas of the Great Lakes (Beeton, 1969). The changes in phytoplankton have been from dominance by multispecies diatom communities to species of green and blue-green algae more tolerant of eutrophic conditions. Zooplankton communities have reacted similarly (Beeton, 1969), resulting in a loss of species diversity and increases in species associated with eutrophic environments. Again, the relation of these changes in fish populations is incompletely understood.

CONCLUSIONS

It is obvious that the environment in many areas of the Great Lakes has deteriorated. Assigning direct cause and effect to changes in specific populations or species of Great Lakes fish is difficult and controversial. Heavy exploitation of many stocks is undoubtedly a factor in the decline of many species. Changes in water chemistry, plankton, bottom fauna, and unexploited fish species, however, clearly show that factors other than fishing have drastically changed the characteristics of the Great Lakes.

Now that we know our capabilities, how can we avoid past mistakes and stop, or perhaps even reverse, the trend toward environmental chaos? One possibility is to understand the forces that operated in the past to produce present conditions. Scientists and administrators with responsibility for protecting the aquatic environment can learn much from the perturbations foisted on the Great Lakes. For example, early recognition of the effects of unmanaged commercial fishing could have prevented, or at least delayed, the decimation of many fish populations. Wise management of the uses of tributary streams would have saved many stocks of anadromous species. It is difficult, however, to blame these errors of omission on our predecessors, for they did not have the advantage of hindsight to improve their foresight. Our generation has no such excuse. Opportunities missed in the past to protect the aquatic communities are gone, but opportunities remain to save and rehabilitate our aquatic environment.

Recognition of environmental degradation in the Great Lakes has led Canada and the United States to a firm commitment to halt and reverse this trend. Evidence of success in this endeavor is already apparent. Rehabilitation of many tributaries has permitted the establishment of spawning runs by anadromous species. Levels of DDT in fish tissue have decreased as much as 80% after the use of the insecticide was banned. More comprehensive and better treatment of municipal and industrial waste has resulted in noticeable improvements in the quality of receiving waters.

Let us hope that by the year 2000 the history of changes in fish species of the Great Lakes will show only increases in native species between 1975 and the new century.

REFERENCES

Aron, W.I., and S.H. Smith. 1971. Ship canals and aquatic ecosystems. Science 174: 13-20.

Baldwin, N.S., and R.W. Saalfeld. 1962 (plus 1970 supplement). Commercial fish production in the Great Lakes, 1867-1960 (supplement 1961-68). Great Lakes Fish. Comm., Tech. Rep. 3. 166 p.

Baldwin, N.S. 1964. Sea lamprey in the Great Lakes. Can. Audubon Mag., November-December, Chap. 19: 535-558.

Beeton, A.M. 1969. Changes in the environment and biota of the Great Lakes, p. 150-187. In Eutrophication: causes, consequences, correctives. National Academy of Sciences, Washington, D.C.

Beeton, A.M., and D.C. Chandler. 1963. The St. Lawrence Great Lakes, p. ___ __ ___. In Limnology in North America. Univ. Wisconsin Press, Madison, Wis.

Beeton, A.M., and W.T. Edmondson. 1972. The eutrophication problem. J. Fish. Res. Board Can. 29: 673-682.

Britt, N. Wilson. 1955. Stratification in western Lake Erie in summer of 1953; effects on the *Hexagenia* (Ephemeroptera) population. Ecology 35: 239-244.

Carr, John F. 1962. Dissolved oxygen in Lake Erie, past and present. Proc. 5th Conf. Great Lakes Res., Univ. Michigan, Great Lakes Res. Div., Publ. 9. p. 1-14.

Carr, John F., and Carl K. Hiltunen. 1965. Changes in the bottom fauna of western Lake Erie from 1930 to 1961. Limnol. Oceanogr. 10: 551-569.

Christie, W.J. 1972. Lake Ontario: Effects of exploitation, introductions, and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29: 913-929.

____________. 1974. Changes in the fish species composition of the Great Lakes. J. Fish. Res. Board Can. 31: 827-854.

Fish, C.J., and Associates. 1960. Limnological survey of eastern and central Lake Erie, 1928-1929. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 334. 198 p.

Hartman, W.L. 1972. Lake Erie: Effects of exploitation, environmental changes, and new species on the fishery resources. J. Fish. Res. Board Can. 29: 899-912.

Hiltunen, Jarl K. 1967. Some Oligochaetes from Lake Michigan. Trans. Am. Microsc. Soc. 86: 433-454.

Hutchinson, G.E. 1957. A treatise on limnology, Volume I: Geography, physics, and chemistry. John Wiley and Sons, New York. 1015 p.

Lawrie, A.H., and J.F. Rahrer. 1972. Lake Superior: Effects of exploitation and introductions on the salmonid community. J. Fish. Res. Board Can. 29: 765-776.

Reinert, Robert E. 1970. Pesticide concentrations in Great Lakes fish. Pest. Mon. J. 3: 233-240.

Schneider, J.C., F.F. Hooper, and A.M. Beeton. 1969. The distribution and abundance of benthic fauna in Saginaw Bay, Lake Huron. Proc. Conf. Great Lakes Res. 12: 1-20.

Scott, W.B., and E.J. Crossman. 1973. Freshwater fishes of Canada. Fish. Res. Board Can., Bull. 184. 966 p.

Smith, S.H. 1957. Evolution and distribution of the Coregonids. J. Fish. Res. Board Can. 14: 599-604.

_________. 1964. Status of the deepwater cisco population of Lake Michigan. Trans. Am. Fish. Soc. 93: 155-163.

_________. 1968. Species succession and fishery exploitation in the Great Lakes. J. Fish. Res. Board Can. 25: 667-693.

_________. 1972. Factors of ecological succession in oligotrophic fish communities of the Laurentian Great Lakes. J. Fish. Res. Board Can. 29: 717-730.

_________. 1974. Responses of fish communities to early ecologic changes in the Laurentian Great Lakes, and their relation to the invasion and establishment of the alewife and sea lamprey. MS in preparation.

Weiler, R.R., and V.K. Chawla. 1969. Dissolved mineral quality of Great Lakes waters. Proc. Conf. Great Lakes Res. 12: 801-818.

Wells, L., and A. McLain. 1972. Lake Michigan: Effects of exploitation, introductions, and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29: 889-898.

Wright, S. 1955. Limnological survey of western Lake Erie. U.S. Fish Wildl. Serv., Spec. Sci. Rep., Fish. 139. 341 p.