EFFECTS OF EXPLOITATION, ENVIRONMENTAL CHANGES, AND NEW SPECIES ON THE FISH HABITATS AND RESOURCES OF LAKE ERIE

by

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FOREWORD

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

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

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

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

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

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K. H. Loftus H. A. Regier

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Effects of Exploitation, Environmental Changes, and New Species on the Fish Habitats and Resources of Lake Erie¹

by

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ABSTRACT

No other lake as large as Lake Erie (surface area, 25,690 km²) has been subjected to such extensive changes in the drainage basin, the lake environment, and the fish populations over the last 150 years. Deforestation and prairie burning led to erosion of the watershed and siltation of valuable spawning grounds. Marsh spawning areas were drained. Lake-to-river spawning migrations of sturgeon, walleve, and other fishes were blocked by mill dams. Accelerated cultural nutrient loading increased total dissolved solids by nearly 50% (1920-70). Phosphate loading reached 469 metric tons per year by the 1950's and continued to increase. The biomass of phytoplankton increased 20-fold between 1919 and 1963. Oxygen demand for decomposition of these algae so degraded oxygen regimes in the western and central basins by the 1950's that the once abundant mayfly nymphs were destroyed and the central basin hypolimnion became anoxic. The sequence of disappearance or severe depletion of fish species was as follows: lake trout, sturgeon, lake herring, lake whitefish, sauger, blue pike, and walleve. Yellow perch are now declining. All resources were intensively exploited at one time or another. Lake trout suffered only this stress, but changes in the watershed significantly stressed sturgeon and lake whitefish. Degradation of the lake spawning grounds, benthos, and oxygen regimes culminated in severe stress by the 1950's on the remnants of the lake herring and lake whitefish, and on the sauger, blue pike, and walleye. Additional mortality may have been imposed on walleye and blue pike fry by predacious smelt that successfully colonized Lake Erie after fist appearing in 1932. The cultural stresses, in the probable order of greatest to least net effects on the fish community of Lake Erie, appear to have been: (1) an intense, opportunistic, ineffectively controlled commercial fishery; (2) changes in the watershed, such as erosion and siltation of stream beds and inshore lake areas, and construction of dams in tributaries; (3) nutrient loading, destruction of biota, and reduction of dissolved oxygen; and (4) the competitive and predatory activities of invading species.

INTRODUCTION

Fish communities and their habitats in Lake Erie have been radically changed over the last 150 years by a series of cultural stresses imposed by man. These stresses have included intensive and selective commercial fishing, watershed and shore erosion, nutrient loading, invasion of new species via canals, and stream destruction and marsh drainage.

Changes in the biological and chemical characteristics of Lake Erie have been particularly marked over the last 50 years: basic lake fertility has

1 Contribution 468, Great Lakes Fishery Laboratory, U.S. Bureau of Sport Fisheries and Wildlife, Ann Arbor, Michigan 48107.

increased measurably; average lake water temperature has increased; striking changes have occurred in the density and composition of phytoplankton; summer oxygen deficits have progressively increased; and the benthos of the western basin has completely changed. Such changes have been the direct result of the ever-increasing nutrient loading of Lake Erie via domestic, industrial, and agricultural wastes. Such cultural eutrophication has been thoroughly documented for other large lakes in the world: Lakes Zurich, Constance, and Leman in Central Europe and Lake Washington in western North America. Nowhere, though, has a body of water as large as Lake Erie aged as rapidly as this lake has, especially within the last 2 or 3 decades. Furthermore, many of the changes are considered irreversible.

Fish populations have also changed greatly since the late 1800's. Some species of fish have virtually disappeared, and new species have appeared and multiplied explosively. Before the 1940's most investigators concluded that the great declines in such valuable Lake Erie species as lake herring, lake whitefish, and lake trout were due mainly to overfishing. Langlois (1941) was among the first to suggest that environmental stresses in Lake Erie-such as the turbidity brought from the farmlands of Ohio and Indiana because of deforestation and poor watershed management-were mainly responsible for great declines in commercial catches, at least in Ohio waters. He was challenged by Van Oosten (1948) who maintained that the principal cause of the declines was the largely unregulated fishery. Nevertheless, since the early 1940's fishery scientists have placed greater and greater significance on the deleterious effect of certain environmental changes caused by pollution and eutrophication on the well-being of fishery resources of Lake Erie. Environmental changes over the past 50 years in Lake Erie have been most recently analyzed and documented by Arnold (1969), Beeton (1961, 1965, 1966, 1969), Carr (1962), Carr and Hiltunen (1965), Davis (1964), Hartman (1970, 1972), Trautman (1957), and Verduin (1964, 1969).

The purpose of this paper is to provide a detailed case history of the changes in Lake Erie's fish populations and their environment since the late 1800's, with the hope of demonstrating the effects of exploitation, changes in the watershed, accelerated cultural eutrophication, the invasion and introduction of new species of fish, and the interactions of these stresses on Lake Erie's native fish populations.

DESCRIPTION OF LAKE ERIE

Lake Erie ranks fourth in surface area among the five Laurentian Great Lakes of North America and is the 12th largest lake in the world. Discharges from Lakes Superior, Michigan, and Huron drain 'through Lake Erie into Lake Ontario and then via the St. Lawrence River into the Gulf of St. Lawrence and the Atlantic Ocean.

Morphometry

Lake Erie is centered at 42°15' N. lat. and 81°15' W. long. It is 388 km long, 92 km wide at its widest point, and has a surface area of about

	В	Basin					
Item	Western	Central	Eastern	lake			
Maximum length (km)	80.5	213.2	136.8	387.9			
Maximum breadth (km)	64.4	92.1	76.4	92.1			
Maximum depth (m)	20.4	25.6	64.0	64.0			
Mean depth (m)	7.4	18.5	24.4	18.5			
Area (km ²)	3,276.0	16,177.0	6,237.0	25,690.0			
Volume (km ³)	24.2	299.2	151.7	475.1			
Shoreline (km)	431.8	504.2	423.7	1,359.7			
Percentage of total area	12.8	62.9	24.3	100.0			
Percentage of total volume	-5.1	63.0	31.9	100.0			
Percentage of total shoreline	31.7	37.1	31.2	100.0			

Table 1. Morphometry of Lake Erie (1).

1 Basin subdivisions: western, from southern tip of Grosse Ile eastward to a line from the tip of Point Pelee to tip of Cedar Point; central, east to a line from the base of Long Point to base of Presque Isle; and eastern, east to the head of Niagara River (see Fig. 1). P&metric measurement from United States Lake Survey Chart No. 3. 1950. Scale 1:1,400.000. Revised. Lake Level Reference Point 570.5 ft. James L. Verber, Franz. Theodore Stone Institute of Hydrobiology, Put-in-Bay, Ohio. (Revised by W. L. Hartman)

25,690 km^2 (Table 1). Its immediate drainage basin covers about 75,000 km^2 . Since the lake receives the outflow of Lakes Superior, Huron, and Michigan, however, its total drainage area is 418,679 km^2 . The annual average inflow from the upper Great Lakes via the Detroit River-5465 m³/sec (193,000 cfs) - represents about 95% of the total inflow. The annual mean outflow to Lake Ontario through the Niagara River and the Welland Canal is 5720 m³/sec (202,000 cfs). The theoretical flow-through or flushing rate of 920 days (Federal Water Pollution Control Administration [FWPCA] 1968) makes water quality of Lake Erie very vulnerable to change by the inflowing water.

The Lake Erie region was glaciated at least four times over the past million years (Hough 1958). After the last Wisconsin ice sheet retreated about 12,000 years ago, the lake basin first became established with drainage through the St. Lawrence River system at a water level 30 m lower than it is today. The present elevation of about 174 m above sea level was established 9,000 to 10,000 years ago (Lewis et al. 1966). The sediment on the lake bed today results from erosion of the pre-existing glacial overburden during the last 12,000 years (International Joint Commission 1969). Geologically, the Lake Erie drainage is primarily marine sedimentary rock, including limestone, dolomite, shale, and sandstone (Hough 1958). More than 15 million tons of inorganic sediment are eroded from the watershed and discharged into Lake Erie each year (FWPCA 1968). The shores of Lake Erie consist primarily of easily eroded banks of glacial till and sand; erosion of this till contributes another 15 million tons of sediment to the lake annually (FWPCA 1968). This situation contrasts with presettlement conditions (before 1800), when streams and rivers were clear and had clean sand and gravel bottoms, and aquatic vegetation grew luxuriantly in bays and other shallow inshore areas. Lake Erie water is bicarbonate and has an average pH of 8.3.

Climate

Lake Erie lies at the boundary of the humid microthermal and humid mesothermal climates discussed by Trewartha (1954). Summers are short, hot, and humid; winters are cold with some snow. At land stations, air temperatures average 21 to 24 C in July and -2 to -5 C in February (FWPCA 1968). Precipitation is spread rather evenly through the year and averages about 86 cm.

Lake Erie is the shallowest, southernmost, and warmest of the Great Lakes. Surface temperatures in midlake reach an average maximum of about 24 C, usually in early August, in all basins; occasionally temperatures exceed 26 C in the western basin. The south shore of the western basin has many estuaries, of which Sandusky Bay is the largest and most productive in terms of fish harvest. Summer temperatures in this bay often exceed 26 C.

Physical descriptions of basins

Of considerable ecological importance is the natural geological division of Lake Erie into three basins (Fig. 1). The western basin is the shallowest and smallest. It has an average depth of 7.4 m, a maximum depth of 20.4 m, represents less than 13% of the total lake surface area, and includes only 5% of the lake's volume (Table 1). It contains many shoals, islands, and rocky reefs. This basin has often been considered by some to have the most important fish spawning and nursery grounds in the entire lake, and is the site of extensive boating, fishing, and other recreational activities. Because it is shallow, and close to such large urban areas as Detroit, Michigan, and Toledo, Ohio, it is more vulnerable to change caused by man's activities than are the central and eastern basins. Flushing time for the western basin is about 60 days (Verber 1957).

The bottom of the western basin is made up of 58% soft gray mud, 17% sand, 12% sand and mud, 7% gravel, 3% bedrock, and 3% clay (Verber 1957). Sand and gravel are common near shore and around the islands, and mud predominates in deeper waters.

The large central basin makes up 63% of Lake Erie's surface area and 63% of its volume. It is considerably deeper than the western basin and has an extensive flat muddy plain 18 to 24 m deep.

The eastern basin, the deepest, has a maximum depth of 64 m and an average depth of 24.4 m. It consistutes 24% of Lake Erie's surface area and 32% of its volume. Muddy bottoms predominate in the deeper waters. Much of the shoreline is precipitous and consists of exposed bedrock and deposits of sand and gravel. Only in this basin do populations of *Mysis relicta* and *Pontoporeia affinis*, benthic crustaceans dating from the ice age, persist in significant numbers.

Thermal cycles

Seasonal thermal cycles vary considerably among the three basins in Lake Erie, chiefly because of the large differences in depth and volume.

The shallow western basin usually freezes over during the winter (typically by mid-December), and water temperatures under the ice become



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Fig. 1. Lake Erie, showing the three main basins. Depth contours are in meters.

isothermal at about 1 C. The ice thaws near the end of March, and surface water temperatures gradually rise to almost 10 C by May 1, 15 C by June, and 24-26 C by early August. The water is usually kept nearly isothermal in summer by wind and currents, although intermittent metalimnions are formed in some years after extended periods of hot, calm weather. Fall cooling begins in mid to late August.

The deeper central basin rarely freezes over completely. Spring warming lags behind that in the western basin by about 1 week; by late May temperatures reach about 13 C and the water column is isothermal. A sharp metalimnion forms in June at about 12 m and gradually sinks as the season progresses. Epilimnetic water warms to a maximum of 24-26 C by early August. The fall overturn usually occurs in late September and the water temperature becomes isothermal at about 1 C in late December. Bottom waters during the summer are much colder in the central basin (9 C) than in the western basin (19 C).

The seasonal thermal cycle of the deep eastern basin closely resembles the cycles in the other Great Lakes. In winter the basin is nearly isothermal at 1 C. When the ice breaks up in the spring in the western and central basins, ice floes usually move east and pack over the eastern basin. Consequently, April and May near-surface water temperatures there lag 18 days behind those of the western basin and 11 days behind those of the central basin. Slight warming takes place during April and early May. The upper waters then warm rapidly, and a relatively stable and thick metalimnion is formed that narrows and sinks as summer progresses. The temperature of the epilimnion reaches nearly 24 C by early August, then starts to drop. The hypolimnetic water warms slowly and reaches 7-9 C before the fall overturn, which usually occurs in November. The water column becomes isothermal by late December.

Ichthyofauna

The fishes of Lake Erie are a mixture of cold- and warm-water forms (Table 2), as one might expect from the diversity of limnological conditions and habitats. At least 138 species have been reported in the lake (Van Meter and Trautman 1970). The cold stenothermic coregonids are represented by lake herring, lake whitefish, and longjaw cisco. Native lake trout were once abundant in the eastern basin (Goode 1884) but have been rare since 1940. Native brook trout propagate in a few cold tributaries and are occasionally found in the open lake. Other salmonids that have been stocked since 1870 but have developed no truly viable populations are coho, chinook, and Atlantic salmon, and brown and rainbow trout.

Limnological classification

No single general limnological classification of Lake Erie is adequate because physical, chemical, and biological conditions vary between basins and in certain localities between inshore and offshore areas. The classification by the International Joint Commission (1969) of the western basin as eutrophic, the central basin as mesotrophic-eutrophic, and the eastern basin as oligotrophic-mesotrophic appears to suitably identify the general lake types

Common name	Scientific name
Alewife	Alosa pseudoharengus (Wilson)
Atlantic salmon	Salmo salar Linnaeus
Blue pike	Stizostedion vitreum glaucum Hubbs
Brook trout	Salvelinus fontinalis (Mitchill)
Brown bullhead	Ictalurus nebulosus LeSueur
Brown trout	Salmo trutta Linnaeus
Burbot	Lota lota lacustris (Walbaum)
Carp	Cyprinus carpio Linnaeus
Channel catfish	Ictalurus punctatus (Rafinesque)
Chinook salmon	Oncorhynchus tshawytscha (Walbaum)
Coho salmon	Oncorhynchus kisutch (Walbaum)
Emerald shiner	Notropis atherinoides Rafinesque
Freshwater drum	Aplodinotus grunniens Rafinesque
Gizzard shad	Dorosoma cepedianum (LeSueur)
Goldfish	Carassius auratus (Linnaeus)
Lake herring or cisco	Coregonus artedii LeSueur
Lake sturgeon	Acipenser fulvescens Rafinesque
Lake trout	Salvelinus namaycush (Walbaum)
Lake whitefish	Coregonus clupeaformis (Mitchill)
Longjaw cisco	Coregonus alpenae (Koelz)
Muskellunge	Esox masquinongy Mitchill
Northern pike	Esox lucius Linnaeus
Northern redhorse	Moxostoma m. macrolepidotum (LeSueur)
Rainbow smelt	Osmerus mordax (Mitchill)
Rainbow trout	Salmo gairdneri Richardson
Sauger	Stizostedion canadense (Smith)
Sea lamprey	Petromyzon marinus Linnaeus
Silver chub	Hybopsis storerianus (Kirtland)
Spottail shiner	Notropis hudsonius (Clinton)
Trout-perch	Percopsis omiscomaycus (Walbaum)
Walleye	Stizostedion v. vitreum (M1tch1ll)
White bass	Morone chrysops (Rafinesque)
White sucker	Catostomus commersoni (Lacepede)
Yellow perch	Perca flavescens (Mitchill)

Table 2. Species of Lake Erie fish mentioned in the text, plus important forage species (see Van Meter and Trautman [1970] for complete list).

present. The effects of differences in basin morphometry on temperature and oxygen regimes and organic productivity in the three basins are considerable, as suggested by Beeton (1965) who tentatively classified the eastern basin as morphometrically oligotrophic.

Alley and Powers (1970), who compared the dry weight of macro-, benthos per unit area in Lake Erie with that in other lakes of North America in the manner of Rawson (1953), concluded that Lake Erie is a well-developed eutrophic lake. Because only 5 of the 28 stations sampled by Alley and Powers were from the least productive eastern basin, however, their assessment would seem to apply primarily to the central and western basins.

ENVIRONMENTAL FACTORS

Environmental changes in Lake Erie that appear to be most directly related to changes in the fish populations are discussed here in the following order: alterations in drainage basin, water temperature, nutrient loading, phytoplankton, zooplankton, oxygen regimes (particularly in relation to their effects on benthic invertebrates), and fish parasites. Changes in the fish populations are discussed in a later section.

Drainage basin

Most of the comments in this subsection are based on the conclusions of Trautman (1957) who reviewed the early literature.

As European man settled the Lake Erie drainage basin during the 1700's and 1800's, he drastically changed the vegetative cover and the dynamics of the drainage. Great woodlands were deforested and broad prairies burned over, and converted to rich farmlands. Land erosion markedly increased: Streams and rivers became turbid; silt covered the once clean and important river and inshore spawning grounds of such fishes as sturgeon, muskellunge, and lake whitefish; and silt eliminated beds of inshore rooted aquatic vegetation in shallow bays of western basin and thus sharply reduced the quality of these nursery areas.. The draining and filling of extensive marshlands destroyed other spawning grounds (e.g. for northern pike and sturgeon). Untreated wastes from sawmills, gristmills, slaughterhouses, steel factories, breweries, and towns were discharged directly into the lake or its tributary streams. Sawdust discharged into Ohio streams was frequently reported to asphyxiate fish when it compacted in their gills. The decomposition in rivers of large quantities of refuse from breweries and slaughterhouses apparently resulted occasionally in low oxygen levels and sizable fish kills. The hundreds of dams built during the mid-1800's for millsites also destroyed fish populations by making many upstream spawning areas inaccessible to sturgeon, walleves, and white bass.

Temperature

Beeton (1961) who analyzed water temperature records from the city water filtration plant at Erie, Pennsylvania, for 1918-58, demonstrated that the moving means of the water temperatures were 0.8 to 1.1 C higher in the 1950's than during his baseline period of 1918-27. Most of this increase occurred between 1925 and 1930. After comparing his moving means of water temperature with moving means of air temperature given for the same 1918-27 period by Thomas (1954), Beeton concluded that the warming trend of the lake followed that of the climate. No significant change has taken place since then. Though certainly not a cultural stress, this unique natural change allegedly affected lake whitefish survival adversely (Lawler 1965).

Transparency

The transparency of Lake Erie water has apparently not changed significantly since the 1920's (Beeton 1961). Characteristically, transparency in the western basin is kept extremely low during the entire ice-free period by silt brought in from farmlands in the Maumee River drainage and from the continual resuspension of sediments by strong winds. In the central and eastern basins, Pinsak (1967) detected a 50% increase in suspended material

from summer to early winter which he attributed to "movement of water from the western part of the lake, seasonal increase in organic material, turbulent storm effect, and vertical circulation of the entire water column as the thermocline lowers and disappears."

Nutrient loading

Accelerated eutrophication or cultural enrichment of Lake Erie has been responsible for a lakewide decrease in dissolved oxygen, especially in the bottom waters during summer. Most of the lake's nutrient load from domestic, industrial, and agricultural wastes is discharged into the western basin via the Detroit, Raisin, and Maumee Rivers. The Detroit River, for example, receives 6.1 billion liters of industrial and domestic waste per day (Powers and Robertson 1966). Oxygen demands are increased directly, to some extent, by sedimentation onto the bottom muds of organic and inorganic materials from industrial and municipal waste discharges. Primarily, however, the demands are increased by the decomposition of the large volumes of phytoplankton that result from the nutrient discharges.

Total concentrations of most major ions have markedly increased in Lake Erie over the last 50 years (Beeton 1961, 1965). Total dissolved solids increased from 133 to 183 mg/l by 1960 (Beeton 1965) and to 198 mg/l by 1968 (Chawla 1971). Concentrations of calcium, chloride, sodium-plus-potassium, and sulfate have increased by 6, 16, 5, and 13 mg/l respectively (Chawla 1971). The increases are from allochthonous sources. The Detroit River, for example, receives enough chlorides in industrial and municipal wastes to increase its chloride content 2 1/2 times (Ownbey and Kee 1967). Kramer (1961) showed that, within the lake, concentrations usually increase from west to east; he suggested the cause to be the loss of water through evaporation as the water mass from the upper Great Lakes flows through Lake Erie.

The major nutrient ions, nitrogen and phosphorus, have also markedly increased since 1930. On the basis of a review of the meager data available, Beeton (1969) concluded that open-lake ammonia-nitrogen increased fivefold and total nitrogen threefold between 1930 and 1958. In the western basin the concentration of ammonia-nitrogen increased about 13-fold, from 13 mg/l in 1930 (Wright 1955) to 170 mg/l in 1967-68 (FWPCA 1968). In the open waters of the central basin ammonia-nitrogen has doubled since 1901 (Lewis 1906; International Joint Commission 1969) and total phosphorus appeared to double between 1942 and 1958. Verduin (1969) cited data from FWPCA showing an average increase of 50% in soluble phosphorus in Lake Erie between 1962-64 and 1967-68; thus concentrations have continued to increase. Within the lake, concentrations of nitrogen and phosphorus, as well as silica, decreased from west to east (FWPCA 1968); for example, during 1967-68 the concentration of soluble phosphate was 51-120 mg/l in the western basin, 15-60 mg/l in the central basin, and 930 mg/l in the eastern basin. This west to east reduction in nutrients reflects the high biological uptake during organic synthesis in the western basin (Beeton 1969).

Virtually all phosphorus in the western basin is allochthonous. Harlow (1966) determined in 1964 that the Detroit River contributed 107,500 tons

of total nitrogen and 47,000 tons of total phosphates per year. Nearly 75% comes from municipal waste discharges, and 66% of that comes from detergents (FWPCA 1968). Curl (1959) estimated that during the early 1950's about 469 metric tons per year were being discharged into western Lake Erie. He found the bottom sediments considerably enriched in phosphorus, and speculated that this nutrient was lost from the western basin chiefly by sedimentation and not by outflow into the central basin. Verduin (1969) reported that the most striking change in western Lake Erie between 1948 and 1962 was the fivefold increase in phosphates. Verduin and others (e.g. FWPCA 1968) argued that this increase in phosphorus has been mainly responsible for today's large phytoplankton crops and the superabundance of the filamentous alga, *Cladophora glomerata*, which is now a major nuisance along the shore in western Lake Erie. The ultimate consequences of such increased organic production has been destruction of summer oxygen regimes.

Phytoplankton

Significant changes since 1919 in the abundance and species composition of phytoplankton in the central basin are directly related to accelerated eutrophication of Lake Erie. Davis (1964), who analyzed phytoplankton counts taken almost daily since 1919 at a water filtration plant near Cleveland, Ohio, found that the average density of phytoplankton has steadily increased from 410 cells/ml in 1920-37 to 1,254 cells/ml in 1944-63 (Fig. 2). This threefold increase has a direct bearing on the cycling of nutrients to



Fig. 2. Phytoplankton abundance (cells/ml) in Lake Erie as measured at the intake of the Cleveland Filtration Plant, 1927-62 (redrawn from Davis 1964).

higher trophic levels (e.g. to fish), and also increases the oxygen demands of the water or mud, or both, to the detriment of certain populations of fish and benthic organisms (e.g. lake herring and the mayfly, Hexagenia).

Seasonal cycles of abundance have also changed. Not only are the spring and fall maxima in the central basin now several times higher than in 1927 (Fig. 2) but the pulses have become considerably longer in recent years (Davis 1964). Summer and winter minima between pulses have concurrently become shorter. Not only do fish planktivores have a more concentrated food supply, but it is available at high densities for a longer and longer period during the growing season. In this sense, the biomass of phytoplankton available to higher trophic levels is at least 20 times greater now than in the 1920's.

Davis (1969) who determined the forms dominating spring and fall phytoplankton pulses in central Lake Erie, showed that the oligotrophic diatom *Asterionella* usually dominated the spring pulse between 1920 and 1949; since then the more eutrophic diatom *Melosira* has been dominant. The fall phytoplankton pulses were dominated by *Synedra* and *Melosira* until 1947. Then the mesotrophic diatom *Fragilaria* began to become important, as well as the green alga *Pediastrum* and the eutrophic blue-green algae *Anabaena* and *Aphanizomenon*. By 1970 the fall pulses were invariably dominated by three eutrophic blue-green algae in *succession - Anabaena, Microcystis*, and *Aphanizomenon*.

Studies by Chandler (1940) and Hahn (1969) showed that the plankton diatom flora around the islands in western Lake Erie changed markedly between 1939 and 1965. Some abundant species such as *Cyclotella stelligera* became rare, and other species such as *Melosira binderana* and *Diatoma penue* var. *elongatum* became considerably more abundant. Quantitatively, the total diatom flora increased greatly. For example, the density (cells/ml) of diatoms was 974, 220, and 1,245 for March, April, and May in 1939, and 8,060, 6,913, and 4,216 for the same months in 1965. These species and density changes show gradual eutrophication of the waters of western Lake Erie, according to Hahn (1969).

The filamentous alga *Cladophora glomerata*, which is attached to bottom materials to depths as great as 5 m, has developed heavy growths along the shores and islands over the last 30 years (Langlois 1945; FWPCA 1968). At times dense growths of *Cladophora* develop on the reefs used during the spring by spawning walleyes. The growths usually develop before all walleye eggs are hatched but the effect of this algal growth on hatching success is unknown. Great quantities of *Cladophora* are frequently broken loose by wave action and currents. When these floating mats settle to the bottom, their decomposition adds significantly to the oxygen demands of the sediments.

Zooplankton

Long-term quantitative changes in zooplankton in Lake Erie as a whole have not been adequately documented, although Bradshaw (1964) did compare data for the island region of the western basin that were collected successively by Chandler (1940, 1942) Hubschman (1960) and Bradshaw and J. Verduin. He showed that zooplankton production in the island area in the western basin markedly increased between 1939 and 1959. Monthly average standing crops of Cladocera were nearly three times higher in 1949 than in 1939 (Bradshaw 1964). In July and August, for example, the number of Cladocera per cubic meter seldom exceeded 7,000 in 1939, usually was between 10,000 and 22,000 in 1949, and usually exceeded 26,000 in 1959 (peaks in 1959 were nearly 110,000 in early July and 85,000 in late August). Total Copepoda were more abundant throughout the 1949 season than during 1939, and adult Copepoda were more abundant in July and August in 1959 than in 1949. This analysis suggests that the quantity of zooplankton in 1959 may have been double that in 1939 and 40% greater than that in 1949.

Differences in zooplankton between the three basins in Lake Erie have been synoptically examined only twice (Davis 1968, 1969). Collections were made at midlake stations along an entire longitudinal transect in July and October 1967, and along part of the transect in January 1968. In July abundance was distinctly highest in the western basin and lowest in the eastern basin, confirming the usual concept that productivity is highest in western Lake Erie. In October, however, the western basin was relatively improverished and zooplankton biomass surprisingly increased from west to east (Davis 1969). Nonetheless, Davis cited a personal communication from Kleveno who showed that quantities of seston, chlorophyll a, and phytoplankton were highest in the western basin and lowest in the eastern basin during October 1967. Davis therefore concluded that the unexpected decrease in zooplankton abundance from west to east during October 1967 did not necessarily contradict the accepted pattern of production rates in Lake Erie, but was more likely the temporary result of some "unrecorded environmental change over the period preceding sampling."

Such increases in organic production in this trophic level over the decades added to the accumulation of algae, and the resultant oxygen demands during decomposition adversely affected oxygen regimes. Certain noticeable qualitative changes have occurred. *Diaptomus siciloides*, which is usually found in eutrophic waters, was rare in Lake Erie in 1929 and 1939, but has now become abundant in the western basin (Davis 1966). On the other hand, the large zooplankter, *Limnocalanus macrurus*, was abundant in 1929 in the eastern and central basins, and even in the western basin during winter and spring, but few were taken during extensive sampling in 1967 and 1968; Gannon and Beeton (1971) believed that depletion of hypolimnetic dissolved oxygen and predation by planktivorous fish were the most probable causes of the decline.

For Lake Erie as well as the other Great Lakes, Patalas (1972) examined the relation between the density of crustacean plankton, the concentration of chlorophyll a in near-surface waters, and the heat content of a O-25 m water column (1 cm² in area; base 0 C). As expected, concentrations of chlorophyll a and densities of crustacean plankton were very high in Lake Erie in June and July when lake heat content was moderate (Fig. 3). Plankton concentrations decreased slightly, however, as heat content rose in August (although the numbers were still higher than in any other lake except Ontario). Patalas (1972) suggested that perhaps the optimal temperature range for maintaining the type of crustacean community that exists in Lake Erie was surpassed in August. He found a general trend towards a decrease in the proportion of



Fig. 3. Relations between crustacean abundance (individuals/cm²), heat content (Kcal/cm²), and chlorophyll *a* concentration in surface waters (μg/1) for four Great Lakes. The bars represent mean crustacean abundance in different parts of the lakes in June, July, and August for Lakes Ontario and Erie and in August for Lakes Superior and Huron (after Patalas 1972).

calanoid crustaceans and an increase in cyclopoids and cladocerans from the most oligotrophic Lake Superior to the most eutrophic Lake Erie.

Deterioration of dissolved oxygen

Oxygen depletion in the western basin was apparently not serious before the critical year of 1953. Dissolved oxygen (DO) was never below 70% saturation in 1928-30 (Wright 1955), or in 193840 (Chandler 1944). That severe depletion did not occur in the western basin between 1940 and 1953 was indicated by the persistence of the oxygen-sensitive nymphs of the burrowing mayflies *Hexagenia rigida* and *Hexagenia limbata occulta*, which dominated the benthos of western Lake Erie before 1953. Verduin (1964) reported that during June each year before 1953, vast numbers of adult *Hexagenia* congregated at the base of lampposts in lakeshore cities, where truckloads of the dead insects were gathered by street cleaners. But 28 days of calm, hot weather during the summer of 1953 caused sufficient stratification to prevent complete vertical circulation and to decimate the population of *Hexagenia* (Britt 1955a). Oxygen demands of the water or bottom muds, or both, were great enough to reduce DO to less than 1.2 mg/l, Values were as low as 0.7 mg/l in the island area,

Low oxygen and destruction of *Hexagenia* nymphs are clearly related. Densities of mayfly nymphs averaged $397/m^2$ in 1929 and 1930 (Fig. 4) $422/m^2$ in 1942 and 1943, and $300/m^2$ in June 1953 (Britt 1955a). But by



Fig. 4. Distribution and abundance of *Hexagenia* nymphs in western Lake Erie, 1930 and 1961 (after Beeton 1965; Carr and Hiltunen 1965). Numbers indicate nymphs per square yard.

September 1953 the population had been greatly reduced. Britt found only $44.3/m^2$ in 61 bottom collections and reported a great reduction in the use of *Hexagenia* nymphs as food by the silver chub. The mayfly population made a short-lived recovery in 1954 to pre-1953 levels. Nymphs were 18.7 times as abundant in the fall in 1954 as in 1953 (Britt 1955b). By 1957, however, the average density was only $37/m^2$ (Beeton 1961) and by 1961 it was less than $1/m^2$ (Carr and Hiltunen 1965). Mayfly numphs are now extremely rare in the western basin. Carr et al. (1965) determined that in 1963 DO was greatly reduced after only 5 days of hot, calm weather. Concentrations were as low as 2 mg/l in bottom waters over nearly 50% of the basin. Daily sampling from June 22 to August 31, 1966 (Britt et al. 1968) confirmed the findings of Carr et al. (1965) and indicated that even more rapid and severe oxygen depletion can be expected in the future. Severe oxygen depletion was again observed in late June 1971 in the western basin by the U.S. Fish and Wildlife Service (unpublished data).

Other major changes in the bottom fauna of western Lake Erie between 1930 and 1961 presumably related to progressive deoxygenation were summarized by Carr and Hiltunen (1965). They concluded: "The most important changes in fauna during the 31-year period were: ninefold increase in Oligochaeta; fourfold increase in Tendipedidae; twofold increase in Sphaeriidae; sixfold increase in Gastropoda; and a reduction *of Hexagenia* to less than 1% of former abundance."

Oxygen levels in the waters of the central basin have also deteriorated. Carr (1962), who analyzed data from various surveys after 1928, inferred that the progressive change was as follows: Sharp thermal stratification was confirmed in the central basin in 1928-30 and DO below 5 mg/l was detected in August below the metalimnion at several localities during those years

(Wright 1955). Fish and associates (1960) also found low values during 1928-29, even though they may not have effectively sampled the narrow hypolimnion, which is often restricted to a stratum within 2 m from the bottom. Lower DO, often below 40% saturation, was found in 1947-53 (Powers et al. 1959). The first observation of an extensive zone of low DO (1-3 mg/l) in the southwestern part of the central basin was made in 1958 (Carr 1962). Synoptic surveys in 1959 and 1960 (Beeton 1963) confirmed that vast areas of the narrow hypolimnion below a sharp thermocline suddenly developed severe DO depletion after thermal stratification became established in early summer. Indeed, in late August 1960 DO was below 2 mg/l in the bottom waters of the western two-thirds (16,777 km²) of the central basin (Fig. 5). In August 1964 the DO in more than three-fourths of the bottom waters of the central basin was only O-2 mg/l (U.S. Public Health Service 1965). Since 1964, mean depletion rates for dissolved oxygen during summer in the bottom waters of the central basin of Lake Erie have continued to increase (Fig. 6). This increase has resulted, for example, in anoxic conditions developing by August 9 in 1970 and remaining for 2 months, until the loss of stratification (Burns and Ross 1971).

The described changes in oxygen regimes in the central basin of Lake Erie are especially important because this region is a key area for certain fish populations. Before anoxic conditions set in, the hypolimnion served as a required oversummering sanctuary for such cold stenotherms as lake herring, lake whitefish, and some lake trout moving in from the deeper eastern basin; it may also have served as an optional intermittent summer sanctuary for blue pike and smelt (Trautman 1957).

Dobson and Gilbertson (1971) determined oxygen depletion rates (milligrams per liter per month) on the basis of data collected in summer in the central basin since 1929. The long-term trend (Fig. 6) indicates that the rate of deoxygenation of the bottom water has increased in the last 2 decades at the approximate annual rate of 0.075 mg liter⁻¹ month⁻¹ year⁻¹ (2.2 μ moles liter⁻¹ month⁻¹ year⁻¹).

Using 110 days as the average duration of summer stratification in the central basin, Dobson and Gilbertson (1971) determined that a depletion rate of 3.0 mg liter-' month-' will cause virtual deoxygenation in the central basin before the fall overturn. They further determined that this critical value first occurred about 1960.

Gilbertson et al. (1972), using 125 days to represent the longest period of summer stratification, determined the critical depletion rate to be about 2.7 mg liter⁻¹ month⁻¹. According to Dobson and Gilbertson (1971) this rate was reached about 1956 (Fig. 6). Gilbertson et al. (1972) in another analysis plotted oxygen depletion rates against estimates of phosphorus loading from municipal sewage and detergents for the entire Lake Erie basin, including drainage from the upper Great Lakes; they found that the critical value of 2.7 mg/l per month was reached in 1955. About 12,000 short tons of phosphorus were then being dumped into Lake Erie each year. By 1967 the municipal phosphorus loading was up to 19,100 short tons per year.

The International Joint Commission has recently proposed water quality objectives that will reduce phosphorus loading of Lake Erie. The specific objective of the "Agreement Between Canada and the United States of



Fig. 5. Distribution of dissolved oxygen (mg/l) in the bottom waters of Lake Erie, August 1960 (after Beeton 1963).



Fig. 6. Estimated mean depletion rates for dissolved oxygen during summer in the bottom water of central Lake Erie, 1929-70. Note that the critical rate of 3.0 mg/l per month, reached about 1960 (based on 112 days as the average period of summer stratification), produces zero oxygen before the end of summer stratification (after Dobson and Gilbertson 1971).

America on Great Lakes Water Quality" (Signed by Prime Minister Trudeau and President Nixon on April 15, 1972) in relation to phosphorus is: "Concentrations should be limited to the extent necessary to prevent nuisance growths of algae, weeds, and slimes that are or may become injurious to any beneficial water use." It is hoped that the future phosphorus loading from sewage and detergents will be reduced to the 1955 level of 12,000 short tons. A further reduction to about 11,000 short tons total loading (including sewage and detergents), would then presumably cause summer hypolimnial conditions in the central basin to approximate those present before 1931.

These considerations by Dobson and Gilbertson (1971) and Gilbertson et al. (1972) have dealt with zero oxygen levels in the hypolimnion before summer stratification ends. However, cold stenotherms that once oversummered in the deeper waters of central Lake Erie (Trautman 1957) cannot tolerate oxygen tensions below 3 to 4 mg/l. Since these levels were obviously reached several years before 1955-60, when total anoxia occurred before the fall overturn of stratification, the stress of low DO was severe on certain fish populations at least by the early 1950's. As I show later, certain fish populations became highly unstable in Lake Erie in the early 1950's;

Critically low DO has not yet been reported from the deep eastern basin. On the basis of meager historical data, Carr (1962) suggested only that the oxygen demand in the bottom waters appeared to increase between 1930 and 1962. In the summer of 1971, however, moderately low oxygen levels of 2-5 mg/l were detected in some deep areas of the eastern basin (Great Lakes Fishery Laboratory, unpublished data). Thus, low-oxygen stress on the benthos and fish communities is becoming significant in this basin.

Sediments of the three basins in Lake Erie differ considerably in their demands for oxygen, and the degree of demand correlates exactly with the chronology of deterioration of oxygen regimes; first in the western basin, then in the central, finally in the eastern. J. F. Carr (personal communication) found that the 5-minute uptake of dissolved oxygen by sediments was 400-600 mg/g of sediments in the western basin, 200-500 mg/g in the western part of the central basin, 25-400 mg/g in the eastern part of the central basin, and 50-400 mg/g in the eastern basin.

Other qualitative changes have recently occurred in the benthos of Lake Erie. Veal and Osmond (1968) showed that by 1967 the abundance of the pollution-tolerant tubificids *Limnodrilus hoffmeisteri* and *L. cervix* had increased in the western end of Lake Erie, indicating a continuing advance in pollution. Their analysis of benthic macroinvertebrates throughout Lake Erie showed that pollution-intolerant mayfly nymphs and caddisfly larvae predominated in the oligotrophic eastern basin, pollution-tolerant tubificids in the eutrophic western basin, and intermediate forms in the mesotrophic central basin.

Brinkhurst et al. (1968), who analyzed collections of oligochaetes from all basins in Lake Erie, found mostly pollution-tolerant forms in the western basin, oligotrophic forms (common in the upper Great Lakes) in the eastern basin, and a mixture of these forms in the central basin.

Fish parasites

Major and relatively rapid changes in the number and variety of parasites of Lake Erie fishes have occurred since the study by Bangham and Hunter (1939). During 1961-69, Dechtiar (1972) found at least one species of parasite in 96% of the 46 species of fish from Lake Erie (1,112 fish examined). The known parasitic fauna of Lake Erie fish now totals 215 species. Ninety-six of Dechtiar's records were new. He suggested that the changes in Lake Erie's environment and fish fauna related to cultural eutrophication and pollution, and the increased abundance in certain species of fish such as smelt and freshwater drum, have directly influenced the changes in parasitic fauna since 1939.

The parasite of greatest concern at the present time is the microsporidian, *Glugea hertwigi*. It was first recorded in 1960 in rainbow smelt (Dechtiar 1965). Since then it has increased in occurrence; nearly 88% of the smelt population was infected in 1971 (Nepszy and Dechtiar 1972). An unusually severe postspawning mortality during May 1971 may have been partly due to the parasite load. Commercial fish production from Lake Erie has been high throughout the history of the fishery. The annual production from Lake Erie has often equaled or exceeded the combined production of the other four Great Lakes. The lake's warm shallow water, its diversity of habitats, and its greater organic richness are undoubtedly responsible for its greater productivity.

Lake Erie has always produced the greatest variety of commercially important fishes among the Laurentian Great Lakes; no less than 19 species have been significant in the landings at one time or another in the more than 150 years since commercial fishing began. From 1915 (when complete fishery statistics were first available) to 1971, total annual production of fish from Lake Erie has been as high as 28.5 million kg (76.3 million lb) in 1915 (Fig. 7) and 28.2 million kg (75.4 million lb) in 1956, and as low as 11.2 million kg (29.9 million lb) in 1929 and 11.6 million kg (31.0 million lb) in 1941 (Baldwin and Saalfeld 1962). Total production averaged about 19 million kg (50 million lb) per year in 1915-69 and did not show a downward trend over the last 2 decades of that period.

Despite such-consistency in the fish production of Lake Erie since 1915, there has been a marked qualitative change in the fishery resources (Fig. 8). The highly valued lake trout fishery of the mid-1800's disappeared long ago. Since 1925, the fisheries for lake herring and lake whitefish and for saugers and blue pike have also disappeared. Today the important walleye population is greatly depressed and the year-class success of walleyes and yellow perch varies widely from year to year.

In place of these lost resources, other species have thrived or even had explosive increases in abundance. Sizable populations of yellow perch, white



Fig. 7. Total commercial fish production from Lake Erie, all species, 1915-71 (from Baldwin and Saalfeld 1962 plus supplement, and agency records for 1969-7 1).



Fig. 8. Commercial production of important Lake Erie fishes, 1915-70, Canadian and United States landings combined.

bass, and channel catfish still exist in the lake. But the fish biomass is becoming more strongly dominated by such lower valued species as carp, smelt, and freshwater drum (Table 3). In the earliest periods for which records are available, lake herring, blue pike, walleye, sauger, and whitefish provided the bulk of the commercial yield; in the 1960's, however, only the walleye remained among the top 10 species in the commercial yield, and then it ranked only sixth in importance (Table 4).

Commercial catch statistics are considered to be reasonably reliable indicators of population trends for some fishes, but not for others. Most legal-sized lake trout, lake herring, lake whitefish, blue pike, sauger, walleye, yellow perch, white bass, and channel catfish caught commercially were always landed, whereas most carp, goldfish, suckers, and freshwater drum were landed only when the fluctuating market demand was favorable. Frequently, only fish in a selected size range (not necessarily the largest) were accepted by the market. Even then, the low prices paid for these fishes did not generate greatly increased effort by commercial fishermen.

Sport fishing has become a multimillion dollar industry on Lake Erie. It has developed largely since the 1940's and continues to expand. Although few angling records are available, some biologists believe that catches of yellow perch and white bass currently exceed 14 million kg per year-and thus equal or exceed commercial landings of these species.

Fishery management has been greatly complicated by the division of jurisdiction over Lake Erie and its resources among five political entities. The International Boundary between Canada and the United States roughly bisects Lake Erie from the western inlet. The Canadian waters lie in the Province of

Period	Lake stur– geon	Northern pike	Lake herring	Sauz ger ²	White fish	Blue3 pike	Wall- eye	Yellow perch	Smelt	Fresh- water drum	White bass	Suck- er ²	Channel catfish ⁴	Carp	Oth- er ⁵	Total pro- duc- tion
1879-19096	1.052	1.356	25,625	3.700	2,402	10.797'		2.791	-	1.061	611	1,350	604	2.480	100	53,929
1910-1919 ⁶	77	1.250	27,201	3.656	2,945	9,277	1.756	3.017		2,499	383	1,120	1.110	7.544	2.015	63.850
1920-1929 ⁶	39	77	14,126	2.437	1,675	11,292	1.577	5,356		2,367	360	1.090	681	3.189	1.476	45,742
1930-1934	39	62	764	1,943	2,094	14,623	2.113	12,382		2.381	447	1.462	700	2,659	1.594	43,263
1935-1939	31	29	1,070	1.414	2,696	18,526	3.515	6,444		3,359	655	980	641	2,689	1,964	44,013
1940-1944	22	37	203	a 7 0	4,058	13.517	3,779	3.869		3,624	553	628	948	2,593	1,744	36,533
1945-1949	25	21	6.067	567	4.701	12,509	5,807	4.245		3,965	701	506	1.093	2.077	2,226	44,510
1950-1954	14	12	475	354	2,297	13.535	7,566	6,784	890	3,492	3,485	661	1,589	3.007	973	45,134
1955-1959	14	14	128	21	749	10,078	10.267	19.540	4.345	4,020	5,092	413	1.770	4.171	733	61.355
1960-1964	4	2	8	1	19	3	1.484	20,219	13,508	5.770	4,111	333	1,484	4,276	792	52.014
1965-1969	1	2			5		941	26,662	13,489	3.465	2,439	224	898	3.241	1,141	52.508
Largest catcl	h 5.187	2,873	48.823	6,181	7.099	26,788	15.405	33,166	19,182	6.880	9,451	2.024	2,228	13,419		76,313
Year of largest catch	- 1885	1908	1918	1916	1949	1936	1956	1969	1962	1961	1954	1930	1917	1914		1915

Table 3. Average combined annual United States and Canadian production (thousands of pounds) of major commercial fishes¹ from Lake Erie for specified time periods, 1879-1964 (after Report on Commercial Fisheries Resources of the Lake Erie Basin, 1966, U.S. Bureau Commercial Fisheries, Ann Arbor, Michigan, 113 p.).

Species that have hsd **an** annual production greater than 1 million pounds.

U.S. catch only until 1952 Catches of walleye and blue pike combined through 1914. 4

⁵ Includes bullhead through 1951.
⁶ Species normally less thee 1 million pounds (goldfish, bullheads, burbot).

, Average for years of record.

Probably composed of 8 to 9 million pounds of blue pike end the remainder walleye.

Order	Year									
of yield	1908 ²	19153	1920	1930	1940	1950	1960	1966		
1	Lake herring	Blue pike	Lake herring	Blue pike	Blue pike	Blue pike	Yellow perch	Yellow perch		
2	Blue pike	Lake herring	Blue pike	Yellow perch	Whitefish	Walleye	Smelt	Smelt		
3	Carp	Carp	Carp	Freshwater drum	Yellow perch	Yellow perch	Freshwater drum	Carp		
4	Walleye	Sauger	Sauger	Whitefish	Walleye	Freshwater drum	White bass	Freshwater drum		
5	Northern pike	Lake whitefish	Yellow perch	Carp	Freshwater drum	Whitefish	Carp	White bass		
6	Sauger	Yellow perch	Whitefish	Walleye	Carp	Carp	Walleye	Walleye		
7	Yellow perch	Walleye	Freshwater drum	Suckers	Suckers	White base	Channel catfish	Channel catfish		
8	Lake whitefish	Freshwater drum	Suckers	Sauger	Lake herring	Channel catfish	Suckers	Suckers		
9	Suckers	Suckers	Walleye	Lake herring	Sauger	Lake herring	Goldfish	Goldfish		
10	-	-	Channel catfish	White bass	White bass	Suckers	Bullheads	Bullheads		

Table 4. Order of yield of the principal commercial species of fish caught in Lake Erie in selected years from 1908-661. ["Suckers" include both white and redhorse species; catches of "channel catfish" usually include some bullheads before 1952.1

 Adapted from Applegate and Van Meter, 1970.
Ranking of yields of all but lake herring inferred in part from descriptive reports (Canadian landings not reported for majority of species).
Ranking of fourth through ninth species based largely on U.S. records; reports of Canadian landings of saugers, freshwater drum, and suckers lacking.

Ontario and the United States waters are divided among four states: Ohio 69%, Pennsylvania 15%, New York 12%, and Michigan 4%. Management of Lake Erie's fishery resources is controlled by each agency within its respective political subdivision.

Presented below in synoptic form are the case histories of selected species of fish in Lake Erie that have fluctuated substantially in abundance or are now unstable.

Sturgeon

Some observers (e.g. Harkness and Dymond 1961) have claimed that overexploitation was the only significant stress on the lake sturgeon population. Because sturgeon frequently caused heavy damage to fishing gear in nearshore waters, they were customarily killed upon capture in the 1800's to eradicate them. Since sturgeon mature very slowly-few spawn before reaching 20 years of age-extensive removal could quickly destroy the resource. The destruction of river and marsh spawning areas during the 19th century by dam construction and land drainage, however, must have also been important in progressively reducing the numbers of sturgeon (Trautman 1957). Incidental catches, low since the early 1900's, have declined even further since the mid-1950's.

Lake trout

In their review of records of fishery resources in Lake Erie before 1900, Applegate and Van Meter (1970) concluded that a moderately large population of lake trout once existed in Lake Erie. In a recent review of the lake trout of Lake Erie, Moenig (1971 MS) noted that Samuel De Champlain wrote in 1615-18 about the Huron Indians making gillnets to capture these trout. The nets were made of small thongs cut from deer skins as described by Samuel Hearne, 1769-72 (Rau 1884). Stones were used for weights and wooden strips for floats (Van Oosten 1936). During the 1700's European settlers around Lake Erie took lake trout with spears, simple seines, and hook and line (Moenig 1971 MS). By the mid-1800's a substantial commercial fishery had developed, but it was generally restricted to the deeper waters in the eastern half of the lake (Davies 1960). Certain records indicated that lake trout were rare in the western basin, uncommon in the western-central basin off Cleveland, Ohio, and common in the eastern basin-although chiefly confined to the deepest waters (Goode 1884). The earliest production data were recorded in 1873, when 77,566 kg (171,000 lb) of lake trout were landed in Ontario. New York, Pennsylvania, and Ontario reported a combined catch of 48,853 kg (107,700 lb) in 1885 and 55,756 kg (122,920 lb) in 1890. The steady decline in total production of lake trout continued in 1899, and few lake trout were taken after the mid-1930's. Native lake trout are extinct in Lake Erie today.

The reasons for such a rapid and virtually total demise of the lake trout have been a matter of speculation, but Applegate and Van Meter (1970) concluded that the logical explanation is overexploitation. They noted that, despite the relatively light fishing pressure, this slow growing, late maturing, long lived fish was highly vulnerable to exploitation, even though fishing was largely restricted to the deeper waters of the eastern basin. Fishing strategy changed over the many decades of fruitful exploitation of the lake trout, starting in the mid-1800's (Moenig 1971 MS). Gill nets were changed from cotton to linen. Gill-net lifters were introduced, greatly increasing fishing efficiency. Boat engines were converted from steam to gasoline and diesel oil, and hulls from wood to steel. Moenig also indicted permissive fishery management, which allowed overfishing for lake trout to continue unhampered for many years after the first signs of decline were seen in the late 1800's.

Although overfishing was the primary cause of the great decline of the lake trout, the ultimate biological extinction of the lake trout population in Lake Erie since the heyday of the fishery was probably due to environmental stresses placed on the species since the early 1900's (e.g. siltation of spawning grounds and destruction of summer oxygen regimes). Lake trout were probably more vulnerable than many other species to such stresses because Lake Erie is at the southernmost extremity of their zoogeographical range (Trautman 1957).

Longjaw cisco

The longjaw cisco is a deep-water form inhabiting the cold waters of the eastern basin of Lake Erie. First reported by Scott and Smith (1962), it has been rarely encountered in commercial landings. Only six longjaw ciscoes were found among hundreds of lake herring in the commercial catch examined at Port Dover, Ontario, in 1946. A few additional specimens were caught in experimental nets by the Great Lakes Fishery Laboratory in 1957. None have been reported since then. The few longjaw ciscoes present were probably removed by the fishery, with the remnants of lake herring and lake whitefish.

Lake herring

The lake herring was an extremely important commercial fish in Lake Erie for many years, beginning in the 1880's. Through the decades of this fishery hundreds of millions of pounds have been landed. It has suffered a severe and progressive decline over the past 25 years, however, and is now of no commercial importance.

A comprehensive examination of fluctuations and abundance of the Lake Erie lake herring between 1867 and 1946 by Scott (1951) showed that production fluctuated violently from the time statistics first became available in about 1880 (Fig. 9). The earliest decline occurred before 1900, in Michigan waters of the western basin. Production fluctuated widely in eastern Lake Erie but remained generally high because Canadian fishermen increased their fishing effort. A precipitous collapse occurred in 1925 and production continued to be extremely low until 1945 and 1946, when a strong but short-lived recovery marked the last time that lake herring were of any real importance as a commercial species in Lake Erie. Less than a thousand pounds were caught each year in 1965-72.

Analysis of the Canadian production of lake herring by counties along the northern shore of Lake Erie (Scott 1951) and the records of production



Fig. 9. Total commercial production of lake whitefish and lake herring from Lake Erie, 1915-65. Average annual catch of each species in 1965-72 was less than 1,000 lb.

from the several states along the south side of the lake (Baldwin and Saalfeld 1962) show that the largest commercial catches were made in the eastern basin and adjacent waters of the central basin. Lake herring were somewhat more widely distributed in the 1880's and 1890's, when Michigan fishermen were landing moderate quantities in the extreme western end of the western basin. By the early 1900's, however, the catches in Michigan waters had dwindled to almost nil, despite continuing increases in production in the eastern half of the lake. Landings in Ohio (primarily from the central basin) and in Pennsylvania and New York (from the central and eastern basins) continued at good levels until the sudden drop in production in 1925.

Beeton and Edmondson (1972) related this progressive west to east increase in lake herring catches in Lake Erie to the levels of pollution or eutrophication, which are greatest in the western end and decrease progressively eastward. They further suggested that, as degradation of the habitat progressed from west to east, lake herring were increasingly restricted to the eastern end of the lake, where they became more vulnerable to commercial fishing. Van Oosten (1930) presented data indicating that lake herring were heavily concentrated in the deep water off Long Point in the eastern basin in the crucial years of 1923 and 1924. He suggested that unusual storms during the spring of 1923 were responsible for developing this unusual concentration. During these 2 years commercial operators fished the population heavily; Van Oosten (1930) stated, "the gill net fishermen followed and in the firm belief that the supply was extremely abundant they fished excessively for the ciscoes, in many cases slaughtering them indiscriminately by the tons." He

finished his analysis with the conclusion that the cisco was "commercially exterminated by overfishing."

Scott (1951) who analyzed commercial catch statistics for lake herring in Lake Erie through 1945, concluded that periods of abundance were mainly due to the presence of exceptionally strong year classes, like that of 1944. He suggested that the size of the spawning stock in the fall of 1943 must have been unusually small, since the 1943 commercial catch was only 55,000 pounds, and that factors other than the size of spawning stock were therefore clearly of major importance in determining the ultimate success of a year class of lake herring in Lake Erie. By "other factors" Scott meant food, predation, disease, excessive silting, mechanical damage due to storm-generated wave action, and unfavorable temperatures that might influence year-class strength during incubation and the early post-hatching periods. He was, however, unable to prove that any one of these factors was strongly related to year-class success.

Another argument (Powers et al. 1959) dealt with air temperatures in March 1921, which were the highest on record for this month up to that time; they were equally high in March 1946 and 1947. Since an increase of only 1 C in water temperature during the last month of incubation advances hatching by 7 days, and lake herring hatched at temperatures of 4 to 11 C starve within 18 days if they do not obtain proper food (John and Hasler 1956) the high temperatures in 1921 may have been very significant. Perhaps, as Powers et al. (1959) suggested, the extremely warm spring in 1921 resulted in an unusually early hatch of lake herring before the normal spring pulse of zooplankton had developed; the starvation of a large part of that year class may have caused or contributed to the drastic decline in production in 1925. Perhaps the same process operated in 1946 and 1947, when no significant year classes were produced despite the presence of a large spawning population from the strong 1944 year class.

Regier et al. (1969) observed that environmental conditions in the western and central basins, primarily those related to low oxygen tensions, have become unsuitable over the last 15 to 20 years for maintenance of the lake herring populations and that no viable recovery of this resource in Lake Erie could have been expected.

Lake whitefish

The comprehensive examination by Lawler (1965) of fluctuations in the success of year classes of Lake Erie whitefish and the probable causes provided most of the material for the case history on this species.

Lake whitefish successfully spawned in the Detroit River and Maumee Bay of the western basin until about 1890 (Trautman 1957) but by 1900 the runs into the Detroit River had apparently been stopped by pollution. The ever-increasing silt load in the Maumee River began smothering whitefish spawning areas in Maumee Bay by 1900, and those populations were essentially destroyed by 1918 (Trautman 1957), leaving only lake-spawning populations to support the expanding fishery.

For many years after 19 15, when complete catch records were first available, whitefish landings from the open waters of Lake Erie were

characterized by alternating periods of high and low production (Fig. 9). Distinctive peaks were similar in form: The catch rose sharply from relatively low levels, was high for 1 or 2 years, and then declined sharply. Analyses of the catches indicated that these peaks in production were produced by the presence of unusually strong, isolated year classes in the fishery. Lawler identified the three strongest year classes after 1923 as those of 1926, 1936, and (especially) 1944.

Intensive exploitation imposed considerable stress on lake whitefish, but only one environmental factor-water temperature-seems to have been important at that time. Lawler (1965) found no correlation between the success of individual year classes and wind, precipitation, turbidity, or water levels. Neither could unusually successful year classes be attributed to the size of the spawning populations or to the planting of hatchery-raised fry. Year-class strength did, however, appear to be directly related to fall and spring water temperatures.

Since Lake Erie is at the southern limit of the distribution of lake whitefish in North America, thermal conditions might be expected to be somewhat marginal for them. Watt (1962) stated that for species in general that live near the geographical boundaries of their range, climate may almost completely regulate numbers in the populations. Price (1940), reporting on the embryonic development of whitefish to hatching at various constant temperatures, stated that the optimum temperature range for incubation is rather narrow, extending from 0.5 to 6.0 C. Higher incubation temperatures reduced the length of fry at hatching, increased the percentage of abnormal embryos that hatched alive, and increased total mortality to hatching. For example, at 8 C only 19% of the eggs hatched, and 25% of these were abnormal; at 10 C only 1% of the eggs hatched and half of these were abnormal. Lawler (1965) pointed out that the narrow incubation temperature range of 0.5 to 6.0 C must limit successful populations of whitefish to waters where fall spawning temperatures and winter incubation temperatures are close. to the freezing point. When he analyzed the success of year classes of whitefish in relation to water temperatures during spawning, incubation, and hatching periods, he found that strong year classes were produced only when certain favorable temperature conditions prevailed: "(1) Fall temperatures should drop early to 43 F (6.1 C), the temperature below which most successful spawning occurs; (2) the temperature decrease to the optimum for development should be steady and not fluctuating; (3) the spring temperature should increase slowly and late, thus providing a prolonged incubation period at near optimum developmental temperatures." The strong year classes of 1926, 1936, and 1944 all developed under these favorable circumstances.

General climatic warming in the Great Lakes region has resulted in an increase of 0.8 to 1.1 C in the mean annual temperatures of Lake Erie since 1918 (Beeton 1961). Lawler (1965) concluded that if Lake Erie continued to warm, whitefish would be even more severely restricted to the deep, cold water of the eastern basin and might become extinct.

Lake whitefish have certain important ecological characteristics in common with the three other Lake Erie species discussed immediately above. They, like lake trout, longjaw cisco, and lake herring, are cold stenotherms at the southern edge of their zoogeographical ranges. They require cold, adequately oxygenated bottom waters for a summer habitat, and relatively silt-free river or lake spawning areas for successful reproduction. And yearclass success is typically more the result of favorable environmental conditions than of spawning stock size.

No one can deny that the populations of whitefish, as well as those of the other species, were heavily fished in Lake Erie. But the progressive sedimentation of river, bay, and open lake spawning areas may have imposed an even greater-perhaps ultimately critical stress-on many of these populations, especially in the western basin. Obviously, many environmental changes adverse to the well-being of these species occurred during the 1800's and early 1900's, especially in the drainage and lake shore areas. Consequently, exploitation should have been reduced by fishery managers to compensate for environmental stresses (Regier and Loftus 1972). Furthermore, progressive decrease in DO in summer in the bottom waters of the western and central basins continually reduced oversummering habitat for these cold stenotherms and by 1955 or earlier the hypolimnion in the central basin became anoxic by the end of summer stratification. It is not surprising that the last major remnants of these populations were confined to the deep eastern basin (Regier et al. 1969) - the basin last affected by sedimentation, degradation of the oxygen regime, and intensive fishing.

Sauger

The sauger was the first of the three varieties of *Stizostedion* in Lake Erie to show signs of becoming commercially extinct. Although it was once rather abundant in the island region of the western basin (Deason 1933) it was never important in commercial landings before 1915. The catch steadily diminished since 1915, when records first became complete (Fig. 10). Few have been taken since 1960 and the sauger has now approached biological extinction in Lake Erie (Applegate and Van Meter 1970).

The remarkable regularity of the decline in sauger landings prompted Regier et al. (1969) to suggest that environmental conditions were important limiting factors. Spawning grounds in streams and inshore waters along the south shore of the western basin, particularly in the Maumee Bay area (Wakeham and Rathbun 1897), could well have become unsuitable because of pollution, siltation, or damming of the streams. Yet the intense fishery on sauger must not be ignored, nor the fact that most of the major environmental changes in the western basin occurred well after the sauger had begun to decline. Nevertheless, in the last few decades before saugers virtually disappeared from Lake Erie, environmental degradation must have placed additional stress on, the remnants of the population. Finally, as Regier et al. (1969) suggested, the mechanism of introgressive hybridization with the dominant walleye may have ultimately eliminated the pure sauger strain.

Blue pike

Blue pike were extremely important to the Lake Erie commercial fishery for many years. Production after 1915 fluctuated violently; annual production exceeded 8.5 million kg (23 million lb) four times and dipped below 2 million



Fig. 10. Total commercial production of blue pike and sauger from Lake Erie, 1915-65. Catches of both species were very small or nil in 1966-72.

kg (5 million lb) seven times before the collapse of the fishery in 1958 and the near extinction of the species in the 1960's (Fig. 10). Although blue pike were subjected to extremely intensive fishing pressure over the entire period, 1915-58, the abrupt, total loss of this resource in the late 1950's suggests the action of some additional powerful stress.

Year-class strength of blue pike varied widely during the critical years 1943-59 (Parsons 1967). The 1944 and 1949 year classes were by far the strongest, together contributing 42% of the total weight of fall blue pike production in 1943-59. The 1939 and 1940 year classes were moderately strong. The last good year class developed in 1954; all later ones were essentially failures.

Despite the almost complete lack of recruitment after 1954, production continued at a relatively high level until the collapse in 1958 (Parsons 1967). The average age of blue pike in the catch in 1957, 1958, and 1959 increased markedly. Growth rates also greatly increased; blue pike in age-group III were nearly eight times heavier and 7.7 inches longer in 1959 than in 1951. Such growth increases led to more rapid removal of immature fish by the fishery-especially those of the 1954-56 year classes (Parsons 1967) - and thus further reduced recruitment into the spawning population.

The precise mixture of stresses that caused the commercial extinction of the blue pike in 1959 and its virtual biological extinction by 1971 is still speculative. Parsons (1967) documented the decline and fall of the commercial

fishery but did not suggest any reasons other than lack of recruitment. Although the distribution of walleyes and blue pike overlapped in Lake Erie, blue pike were most abundant in the deeper and colder waters of the central and especially the eastern basin. Regier et al. (1969) suggested that the summer reduction of dissolved oxygen in large areas of the central basin forced blue pike to become more restricted to the eastern basin. Indeed, while United States catches from the central basin decreased steadily from 1949 to 1958 (Parsons 1967), Canadian catches from the eastern basin were larger than ever in 1954-56, before the collapse of the fishery in 1958 (Davies 1960). The real cause of year-class failure that started about 1954 was probably the reduction of the population, by heavy exploitation, to a level where environmental factors began to strongly influence hatching success and the survival of young. Regier et al. (1969) suggested that the final "mopping up" phase of the disintegration of the blue pike population was genetic desegregation between blue pike and the numerically dominant walleye, and ultimate disappearance of blue pike during introgression with the walleye.

Walleye

Historically, according to Langlois (1945), Lake Erie walleyes "formerly ascended each spring the Huron River nearly to Ann Arbor, Michigan, the Maumee River to 'Les Grandes Rapides,' the Sandusky River to the rapids at Fremont," and in the central basin "the Cuyahoga River to the rapids above Akron, the Grand River to south of Geneva, and other streams." By 1945 these populations had been for the most part destroyed by mill dams blocking migration routes, siltation and excessive pollution over the spawning grounds, or irregularity in stream flows due to man's activities (Langlois 1945).

The remaining lake-spawning walleye has long been a valuable commercial and sport fish in Lake Erie. Although pronounced annual fluctuations in yield were typical, no long-term trends were recognizable until the mid-1930's (Fig. 11). The landings, which at that time were between 0.4 and 0.8 million kg (1 and 2 million lb) per year, increased sharply and steadily to a peak of nearly 6 million kg (16 million lb) in 1956 before they declined precipitously. The catch fell below 0.4 million kg (1 million lb) in 1963, and then steadily declined to 180,000 kg (470,000 lb) in 1969.

The patterns of decline in blue pike and western basin walleyes were rather similar and may reflect the consequences of a similar mixture of stresses from exploitation, eutrophication, and the appearance of new species in the ecosystem.

The decline of the walleye fishery in Lake Erie was examined in detail in two recent publications: Regier et al. (1969) considered the long-term ecology and management of the walleye in western Lake Erie, and Parsons (1970) dealt more specifically with production and year-class strength during the period 1942-62.

During the crucial years of the rise and fall of the walleye population (1942-61) a significant change occurred in the contribution of year classes to the fishery. Parsons (1970) discovered that, with only two exceptions, the



Fig. 11. Total commercial production of walleye from Lake Erie, 1915-71.

year classes in 1942-61 (as determined from the analysis of trapnet catches in Ohio waters) could be divided into a series of strong year classes in 1942-53 and a series. of weak year classes in 1953-61. The average contribution of the 1942-52 year classes to the commercial fishery was 982,182 fish, whereas that of the 1953-61 year classes was only 185,677. The strongest year class (1948) contributed 1,385,000 walleyes, whereas the weakest (1960) contributed only 3,000. Parsons (1970) noted that the decline in the strength of year classes after 1953 was accompanied by a decrease in the numbers of years during which a year class contributed to the fishery. For example, the strong year classes before 1954 contributed significantly to the fishery for up to 3 years, whereas the later weak year classes contributed materially to the fishery for only about 1 year. As year classes declined in strength after 1954, the growth rate of walleyes increased and the average age of fish cropped by the trapnet fishery decreased. Parsons (1970) suggested that most of these faster growing walleyes were removed from the lake shortly after they reached the legal size (33 cm or 13 inches in Ohio during most of the period). Data presented by Wolfert (1969) show that progressively fewer females would have reached maturity before they were caught by the fishery.

Fishing intensity greatly increased during this crucial period in the 1950's (Regier et al. 1969). Before 1950 the walleye fishery was dominated by trapnet fishermen operating in U.S. waters of Lake Erie. In 1948, however, Canadian fishermen began converting from cotton to nylon gill nets and greatly increasing the amount of gear fished. In addition, the use of fish-finding sonar and ship-to-ship radio was greatly augmented. According to Regier et al. (1969) these improvements in fishing operations and a "laissez faire management policy permitted gill netters, particularly in Ontario, to increase their effectiveness in taking walleyes about 50-fold." Larger and larger

catches of walleyes were taken during the 1950's, primarily in Canadian waters, until the fishery began collapsing in 1957.

As mentioned earlier another significant phenomenon during the 1950's was the degradation of the oxygen regimes in Lake Erie. Periods of oxygen depletion in the bottom waters of western Lake Erie caused a catastrophic decline in the population of mayfly nymphs in 1953. Also in the 1950's dissolved oxygen was being seriously reduced in the bottom waters of the central basin of Lake Erie during summer stratification.

The severe decline of the walleye population in Lake Erie has thus been ascribed by Regier et al. (1969) and Parsons (1970) to overfishing and degradation of the environment via siltation of spawning areas, destruction of oxygen regimes in the western and central basins, and major changes in the benthos in those basins. Regier et al. (1969) proposed a third reason for the decline which was related to the newly established rainbow smelt population. Smelt presumably entered Lake Erie via the Detroit River from an earlier introduction in the Lake Michigan watershed, and were first reported in Lake Erie in 1932 (Van Meter and Trautman 1970). Incidental catches suggested that a sizable population had already become established by the early 1950's (Fig. 12) especially in the central and eastern basins. When fishing intensity for smelt markedly increased in 1960, annual landings of 12 to 16 million pounds per year became common. Adult smelt appear to have proliferated in the cold-water areas in Lake Erie formerly occupied by lake herring. Immature smelt, however, occupy some of the warmer epilimnetic waters of the central and eastern basins during the summer (MacCallum and Regier 1970) living with walleye and formerly blue pike. Regier et al. (1969) argued that pressure from this rapidly increasing smelt population placed a significant additional stress (especially in the central basin) on the walleve population, along with exploitation and eutrophication. Degradation of Lake Erie's environment has



Fig. 12. Total commercial production of rainbow smelt from Lake Erie, 1952-71.

not progressed so far that the walleye will soon become biologically extinct; relatively strong year classes have been produced by small spawning populations as recently as 1970 and 1972. Obviously the environment still favors high spawning success under certain conditions.

Whatever the proportional combination of stresses, evidently by the mid-1950's the high rate of exploitation of the blue pike and western basin walleye had nearly or fully utilized the biological potential of the populations. When the increasing stresses exerted by the degrading environment and proliferating populations of smelt reached a point where fishing and natural mortalities exceeded the replacement capability of the populations, the sudden declines occurred that have been demonstrated also in other stocks (Ricker 1963).

The irregularity in year-class strength from year to year has increased since the 1950's (unpublished data). On the basis of capture of young-of-theyear in experimental trawls, year classes of walleyes were markedly stronger in 1959, 1962, 1965, 1970, and 1972 than in any intervening years. For example, the 1962 year class (the strongest during the 1959-72 period) was 74 times stronger than the 1960 year class (the weakest), and the five strong year classes averaged 7.1 times stronger than the eight weak year classes.

The discussion to this point has dealt primarily with walleye populations from the western basin; a smaller population is largely confined to the eastern basin, Tagging studies have shown that adult western basin walleyes rarely move to the eastern basin (Wolfert 1963), or vice versa (unpublished data).

Production of walleyes from the eastern basin population was negligible before 1953, averaging about 7,500 kg (20,000 lb) per year. Landings have greatly increased since then and held steady at about 41,000 kg (110,000 lb) in 1965-71. The stability of this population is indicated by the continued good representation of fish from much older age groups than are present in western basin landings (Wolfert 1972 MS).

Several factors seem to explain the persistence of walleyes in the eastern basin. Most walleyes are taken in U.S. waters, and fishing intensity there is at an all-time low; management regulations of the State of New York are restrictive and protective; and the effects of accelerated eutrophication have been least in the eastern basin, where dissolved oxygen concentrations in the hypolimnion during late summer are still favorable for fish. Although concentrations of smelt are heaviest in the eastern basin (MacCallum and Regier 1970) and although Regier et al. (1969) suggested that smelt contributed to predatory pressure on young walleyes, the pressure, if it exists, obviously has not been great enough to suppress the walleye population. Substantial increases in abundance of walleyes and smelt have paralleled each other since the early 1950's.

Yellow perch

Yellow perch have long been an important species in Lake Erie; annual landings in 1923-72 have averaged 2.6 million kg (7 million lb), and often exceeded 4.5 million kg (10 million lb) during the early 1930's (Fig. 13) when fishing effort shifted from the declining lake whitefish stocks to this species. By the late 1950's, after not only lake whitefish but also lake herring



Fig. 13. Total commercial production of yellow perch from Lake Erie, 1915-71.

and blue pike had virtually disappeared, the importance of yellow perch to commercial fishermen increased considerably. Strong consecutive year classes in the late 1950's brought average annual production to the high level of about 9 million kg (25 million lb). Although, after 1959, strong year classes occurred only in 1962, 1965, and 1970 (unpublished data), the strong 1965 year class, combined with heavy Canadian, fishing pressure, led to the record production of about 12.6 million kg (23 million lb) in 1969. Production then declined to about 8.6 million kg (23 million lb) in 1970 and 7.7 million kg (17 million lb) in 1971, and is expected to decline much further in the immediate future because the 1971 and 1972 year classes were both weak.

Irregularity in year-class strength has been characteristic of yellow perch in western Lake Erie since the late 1950's. During the period 1959-72, strong year classes were produced only in 1959, 1962, 1965, and 1970 (unpublished data). Coincidentally, walleyes produced their strongest year *classes in* these same years. Regier et al. (1969) commenting on this synchrony, suggested that dominant year classes of yellow perch can exert, 3 years after hatching, a predatory pressure on young-of-the-year walleyes that forces, **walleye** abundance into a 3-year cycle. Since 1959, however, strong year classes of walleyes and yellow perch have been established at a 3-year, 3-year, a 5-year, and a 5-year cycle, in that order, Environmental factors-especially temperature during spawning and incubation periods of walleyes, and perhaps also of yellow perch-would seem to be much more important than interspecific mechanisms in determining year-class success of the two species.

Warm-water species

Strictly warm-water species have not suffered great declines in abundance in Lake Erie over the past 50 years. Although the information on

these species is scanty, it appears that the populations of white bass, channel catfish, brown bullheads, gizzard shad, alewives, spottail shiners, emerald shiners, carp, and goldfish have remained fairly stable during at least the last few decades.

The spawning habits of these species allow them to avoid or at least largely minimize the stresses of sedimentation and low oxygen that affect cold-water bottom spawners. These fish usually spawn in water shallower than 3 m. Some species construct nests, and fan and guard the eggs during incubation; others lay their eggs on vegetation off the mud bottom; and still others lay semibuoyant eggs that incubate off bottom, in the water column (general references are Breder and Rosen 1966; Carlander 1969; Scott 1967). The short incubation period of the eggs of most of these species-often less than 5 days-also minimizes exposure to sedimentation, low oxygen, disease, and predation.

The freshwater drum appears to be significantly favored by the changing environmental conditions or the declines in populations of predators and competitors. Its numbers have steadily increased in western Lake Erie since the late 1950's. The eggs are semibuoyant and float at or near the water surface, and thus avoid potentially deleterious conditions on the lake bottom. Newly hatched larvae also tend to remain near the surface. Fishing pressure is almost nil because freshwater drum have little or no commercial value at present, and scant appeal to sports fishermen.

Colonizing species

The sea lamprey was first reported in Lake Erie in 1921 (Van Meter and Trautman 1970), evidently having invaded the lake via the Welland Canal. Although selective predation by the sea lamprey has decimated the populations of certain valuable commercial fishes in Lakes Superior, Michigan, and Huron (Smith 1968), the sea lamprey has never become abundant nor a serious mortality factor in Lake Erie; evidently the dearth of suitable spawning tributaries has restricted its numbers.

The alewife was first reported in Lake Erie in 1931 (Dymond 1932) and apparently came from Lake Ontario via the Welland Canal (Smith 1970). It has never become numerous in Lake Erie, presumably because of the abundance of predators or the low temperature of the water in the winter and spring. Although certain predators have greatly declined (e.g. walleye and blue pike), the freshwater drum preys on alewives (Price 1963). Smith (1968) noted that deep-water regions where alewives could concentrate in the winter to avoid unfavorably cold water are limited in Lake Erie, and P. J. Colby (personal communication) suggested that alewives very likely suffer cold-water stress in many areas of Lake Erie during the spring thaw and turnover.

Although various salmonids have been introduced, mostly as fry, into Lake Erie since 1870, no important naturally reproducing populations have developed, Apparently one or more of the following factors were responsible: too few fish, or fish of poor quality, of the wrong size, or lacking home-stream imprinting, planted at the wrong site or depth or in the wrong season. Small numbers of lake-run rainbow trout reproduce in several New York streams. After a 30-year interruption in salmon introductions in Lake Erie, about 115,000 fingerling coho salmon, 5-7 inches long, were released in tributary streams along the south shore in spring 1968, 227,000 in 1969, and 526,000 in 1970. The justification for these introductions of high-value fishes centered on the need for a terminal predator in Lake Erie to augment the lost or diminished populations of blue pike and walleye, and to improve sport fishing.

The results of this introduction of coho salmon are not yet clear. As many as 25% of the fish in small individual plantings have survived to be caught by anglers or to return to streams to spawn. Growth has been relatively good; spawning adults averaged nearly 6 pounds after 2 years in the lake. A summer sport fishery has not developed in United States waters, however, because the salmon migrate to the deep cold waters along the Canadian shore during the summer (Russell Scholl, personal communication). Another factor of possible consequence is the relatively higher turbidity in Lake Erie than in Lake Michigan, and the resulting lower visibility of baits or lures. Little information exists on the effects of coho salmon on resident fish populations, although it is known that they feed extensively on emerald shiners and smelt.

SUMMARY

The fish community of Lake Erie has changed dramatically over the past century. The valuable lake trout, lake sturgeon, lake herring, lake whitefish, blue pike, and sauger have virtually disappeared. The walleye population in the western basin has collapsed, the yellow perch are in decline. Thus the salmonids were the first to be overstressed, then the coregonids, and now finally some of the percids. The nearshore waters remain favorable for centrarchids (smallmouth bass) and serranids (white bass) and are becoming more favorable for sciaenids (freshwater drum) and cyprinids (spottail shiners). Other species, such as carp, and the colonizing alewives and (especially) smelt, have shown recent increases.

The extensive changes in fish populations have resulted from four types of stress: exploitation, changes in the watershed, nutrient loading, and the introduction of new species.

All of the disappearing resources have been subjected to intensive exploitation, and this must be considered the primary long-term stress. Its effects have been direct and visible. It was probably the only stress that caused the initial and primary decline of the sturgeon and lake trout.

Changes in the watershed were especially drastic during the 1800's. Removal of the forest and grassland cover for the development of farmland permitted widespread erosion. Stream and bay spawning grounds of sturgeon, walleye, lake whitefish, northern pike, muskellunge, and other species were silted, and luxuriant vegetation in the bays was eliminated by the turbid water. Dozens of mill dams built during the 1800's blocked lake stocks of sturgeon, walleye, and white bass from some of their historical spawning areas. These changes in the watershed destroyed some populations and severely stressed others. Nutrient loading was a consequence of cultural eutrophication. During the 1900's it resulted in greatly increased production of algae and then to the depletion of dissolved oxygen. This depletion was accompanied by the destruction of dense populations of *Hexagenia* in the western and central basins and the loss of oversummering sanctuaries in the hypolimnion for such cold stenotherms as lake herring, lake whitefish, lake trout, and blue pike. Although this stress developed slowly and subtly, its damage to the fish community may have been as great as, or greater than, intensive exploitation. Only marked reductions in nutrient loading of Lake Erie will restore dissolved oxygen in the hypolimnion to levels high enough to support fish life.

The fourth stress on the indigenous fishery resources-the introduction or invasion of new species-has not been particularly damaging in Lake Erie. The alewife and sea lamprey have never become abundant. Carp and goldfish have thrived only in the western basin. Recently introduced coho salmon have shown fair growth and survival; at current stocking rates, however, their effect on resident fish populations is essentially unknown but probably small. Among the new species, smelt may have had the greatest impact, but whether their total long-term effect will be positive or negative is still open to question.

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