THE ECOLOGY AND MANAGEMENT OF THE WALLEYE IN WESTERN LAKE ERIE

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THE ECOLOGY AND MANAGEMENT OF THE WALLEYE IN WESTERN LAKE ERIE

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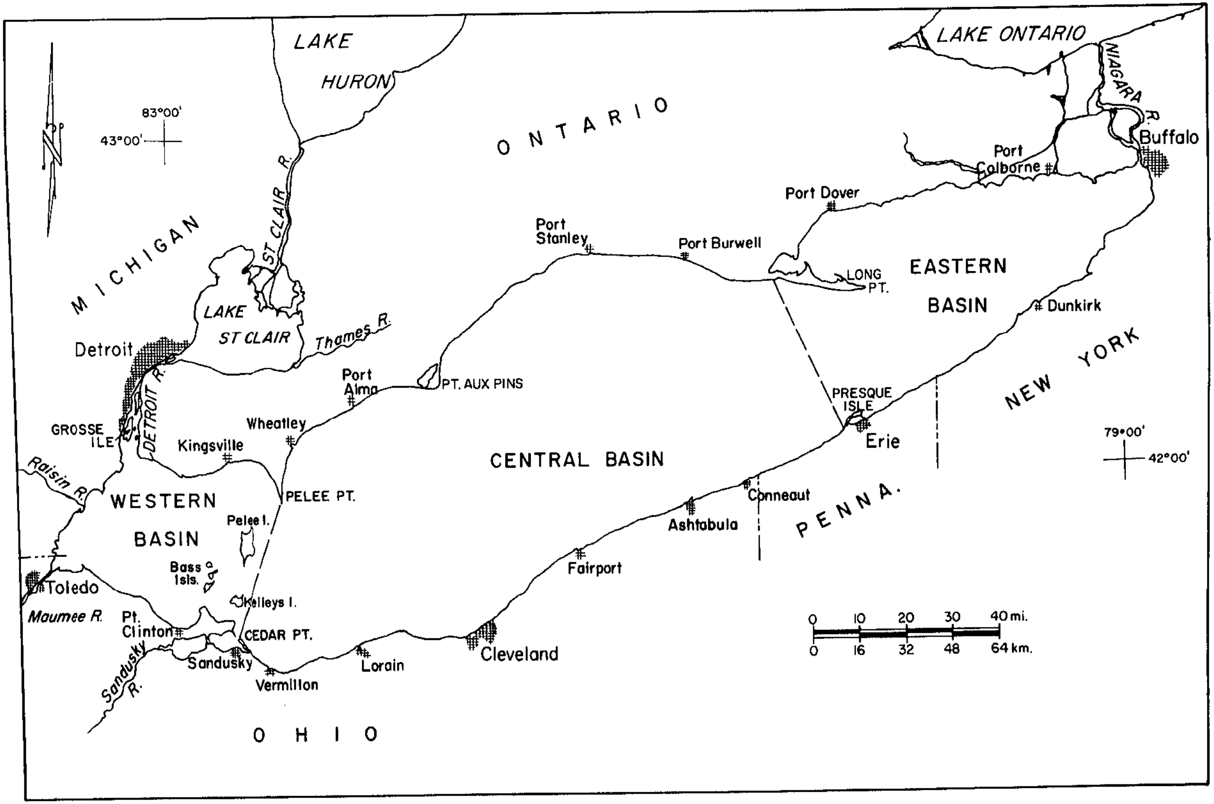

Map of Lake Erie showing key geographic and cultural features. (Adapted from various U. S. Corps of Engineers charts.)

FOREWORD

The public agencies responsible for the management of the fisheries in western Lake Erie have been concerned for many years by the violent instability of the fish resources and the succession of species that have become either economically insignificant or biologically extinct. These problems have also drawn the attention of a number of international commissions. Not once have these efforts led to a common management approach by the various governments with responsibility in this area. Short -run self-interest appears to have blocked cooperation to the ultimate disadvantage of all users.

Concern became acute, a decade ago, with the collapse of the population of the walleye-a species that was then not only the most valued one to commercial and sport fishermen but also the last of the “high value” fishes remaining in the lake. Research programs were begun, fishermen were interviewed, fishery experts consulted, but no common agreement could be reached as to the cause or causes of the changes in the fish populations or the kind of concerted action that might be taken to improve matters.

The report that we present here is a reasonably comprehensive summary of information bearing on the problem of the walleye in western Lake Erie. The information is organized to permit evaluation of all the major hypotheses that have been suggested recently as explanations for the observed fluctuations in the walleye population. Those hypotheses that we believe to be correct are identified and presented in a conceptual framework that we hope will be useful not only for the purpose of current management of the resource but also as a guide for future research. We are aware of the existence of data relevant to the problem of the walleye in western Lake Erie that still have not been analyzed from the standpoint of the views proposed here; when these data and new information are evaluated we expect that some of our present inferences and judgments will be found to be incorrect or, at least, inadequate. Nevertheless, we present this analysis with confidence as an adequate basis for the much needed management decisions that are required at this time if the walleye resource of western Lake Erie is to be preserved.

In acknowledging here a special indebtedness to a number of persons for data, observations and comments made available to us, we do not wish to imply that these persons necessarily subscribe

to all the inferences we have drawn. We thank W. D. Addison, F. M. Atton, N. S. Baldwin, M. J. Brubacher, K. D. Carlander, R. M. Christie, W. J. Christie, J. L. Forney, F. E. J. Fry, M. Hosko, L. J. Johnson, H. Julian, W. H. Krause, K. H. Loftus, J. B. Moyle, N. R. Payne, E. C. Raney, L. L. Rock, W. B. Scott, L. L. Smith, S. H. Smith, and others.

The study received financial support from the Ohio Division of Wildlife, the Ontario Department of Lands and Forests, and the Great Lakes Fishery Commission. Unpublished data from the files of the state and provincial agencies and the U. S. Bureau of Commercial Fisheries were placed at the disposal of the authors by the collaborators in this study.

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"The time has come," the Walrus said
"To talk of many things:
Of shoes-and ships--and sealing wax-
Of cabbages--and kings--
Of why the seas are boiling hot-
And whether pigs have wings."

* * *

But answer came there none-
And that was scarcely odd, because
They'd eaten every one.

Abridged from Lewis Carroll's
"The Walrus and the Carpenter"

SUMMARY AND RECOMMENDATIONS

The objectives of this study were to identify the major factors that have acted to limit the value of the walleye resource in Lake Erie, and to infer how one or more of these major factors might be managed to enhance that value for contemporary and future users.

A preliminary analysis of the reasons for the decline in walleye catches led to identification of four possible major factors: natural evolutionary processes; changes in the Lake Erie biological system due to pollution, enrichment, . . . ; changes in the biological system due to introduction of new species such as smelt, alewife, . . . ; and man's exploitation of the fish resource. We have examined each of these possible factors, but not under these specific headings *or* in this order. Instead, we chose a format that appeared to be more efficient in demonstrating their interrelations.

On occasion we thought it necessary to discuss aspects of the Lake Erie system not closely related to the walleye but essential to an understanding of the effect of one or more of the factors considered to be relevant to the walleye decline. For example, two forms closely related to the walleye, the blue pike and sauger, were once abundant in Lake Erie but now are almost entirely absent. Blue pike populations experienced a "collapse” at least a year before the walleye declined; the abundance of sauger fell off much more gradually over a number of decades. We doubt that the three events were due to different, independent causes and provide evidence that all three suffered from changes in various aspects of their environment including the activities of new fish species and the predator -man. We also suggest that the puzzling disappearance of the blue pike and saugers may have been accelerated by introgressive processes among the three *Stizostedion* species.

We believe that introgression occurred between walleyes and saugers and walleyes and blue pike in the 1950's when the walleye was abundant and the numbers of blue pike and saugers had fallen to record lows. We ascribe the original collapse, or decline, of the blue pike and sauger to other factors, and suggest that introgression was effective in “mopping up” the remnants of these forms. The detrimental effects of introgression would not be as evident in the more abundant walleye.

Our review of the ecology of the walleye indicated that it is a fish typical of middle-aged lakes that are fairly rich in species and somewhat turbid, but have sufficient areas of clean bottom and high oxygen concentration for them to spend much of the time resting on the bottom, and sufficient equally clean areas for successful reproduction. We infer from various data that pollution and enrichment have acted to depress the walleye population and related forms in Lake Erie but not sufficiently to explain the extent of the declines. Relatively large areas of western Lake Erie seem still to provide favorable conditions for walleyes. We do not, however, expect that walleyes will again become as abundant as they were in the early 1950's; that level of abundance seems to have been the consequence of a unique set of factors that are not likely to occur simultaneously again. In fact, we see in such abundance not a symptom of health of the whole fish system but rather a system disruption. A valid analogue might be a sharp increase in a man's weight leading to obesity not being indicative of health but rather of an undiagnosed disease.

We believe that the sharp fluctuations in numbers of the different species in Lake Erie imply disruptions in the interrelations among the fishes, many of which are traceable to a highly exploitive and essentially unregulated fishery. "Unregulated" here refers to the absence of biologically meaningful controls with which conventional political regulation may have relatively little in common. The view that a fishery may have little effect on a population or group of populations seems to be unique to a group of biologists that had some influence over Great Lakes fishery management from about 1940 to 1965. We know of no other group of biologists anywhere in the world that has held similar views in recent times. We have chosen to go into this problem in some detail since their advice, enshrined as management policy, was still being followed to some extent in 1967.

Our analysis of past events of the fish populations and fishing in Lake Erie convinced us that the influence of the fishery has been massive, even as early as about 1865. At that time, the then worthless sturgeon was diminishing in abundance under a "catch-and-destroy" management policy. By the turn of the century the United States fishermen had essentially eliminated the sturgeon and greatly reduced the muskellunge, smallmouth bass, lake trout, and lake whitefish populations. Early in the present century, the lake herring and blue pike fisheries began to fluctuate violently and never again became stabilized. All of these events seem largely attributable to an exploitive and essentially unregulated fishery in United States waters. On the other hand, Canadian waters were, until about 1915, relatively unexploited by comparison and thus for a time formed a partial sanctuary for such migratory stocks as lake whitefish, lake herring, and blue pike.

Following economic collapse of some United States fishing companies before 1900, a series of restrictive regulations was enforced and a nominal hatchery program was expanded. These measures did not save the lake trout, whitefish, and lake herring stocks perhaps because the regulations of the different jurisdictions were uncoordinated. It has never been shown that the hatchery program was in general successful, although we believe from indirect evidence that in some years, for some species, the program did extend the life of the resource.

We ascribe the collapse of the walleye stocks in the 1950's to a combination of limnological changes in the Central Basin, the population explosion of smelt (which was possible, we suggest, largely because of system instabilities traceable to the nature of the fishery), and the direct action of the fishery for the walleye, which became much more intensive in the 1950's due to the entry of a large, technologically advanced Canadian gill net fleet. The collapse of the walleye populations followed soon after. The argument ascribing this collapse to these causes is somewhat too involved to permit convenient summary.

That irreversible limnological changes in the Western Basin were not solely to blame for the collapse can be inferred from the fact that a number of relatively large year classes of walleye have appeared in the Western Basin during the past decade. We would not expect strong year classes if the environment had become permanently submarginal for the walleye.

The fate of recent year classes (regardless of abundance) was almost complete extinction during the first two fishing seasons after reaching a size vulnerable to 3-inch gill nets. Very many fish shorter than 14 inches (total length) were taken when gain from growth far exceeded loss from natural mortality. Hence, we submit that permitting these fish another year or two of freedom would not only increase the value of the resource, but also help to ensure more even reproductive success in the total population. It would help further to reduce the tremendous populations of small yellow perch, alewives, gizzard shad, and other species that offer competition for food and space.

The main events of the past 50 years in the walleye fishery are as follows: The fishery was dominated first by Ohio pound netters who then were superseded by trap netters. Though large numbers of trap nets were fished, the intensity did not appear excessive. Trap net technology was relatively static. Beginning in 1948, a series of technological changes and a laissez-faire management policy permitted gill netters, particularly in Ontario, to increase their effectiveness in taking walleyes, perhaps as much as 50-fold. Large catches were made for a succession of years. Contemporaneously, a series of changes occurred in the abundance of various fish species (smelt, yellow perch, and white bass increased; blue pike and sauger diminished) which we believe to be related to walleye numbers. The walleye population collapsed and has not rebounded in strength, We believe the walleye population would now be larger and the fishery more valuable had recent moderate to strong year classes not been taken in large numbers in gill nets set ostensibly for yellow perch and white bass.

To find further support for our inferences about western Lake Erie walleyes, we examined available information on the fate of populations in Lake Huron's Saginaw Bay and Lake Ontario's Bay of Quinte. We found that the three ecosystems differed substantially and hence we did not expect close similarity in recent events. The evidence that walleyes may have collapsed without a subsequent recovery in Saginaw Bay and Bay of Quinte does not imply that we need to expect the same to happen in Lake Erie. The fact that a number of moderate to strong year classes of walleyes have appeared in Lake Erie subsequent to their abrupt decline in the late 1950's suggests to us that they could have recovered had the fishery permitted it.

We are optimistic about the intensified pollution abatement programs currently in effect on Lake Erie. The view propagated by some persons that once a lake becomes polluted it is "dead" is simply wrong. Lakes can recover, and the Western Basin of Lake Erie might recover rather rapidly under intelligent management . The suggestion has been made that Lake Erie be given over for the mass production of industrial fish. Under such a policy, predators like the walleye, yellow perch, and white bass should be eradicated. This suggestion collides head-on with the objective of the agencies sponsoring this study which is to find a way of maintaining or recovering the valuable walleye resource.

We recommend that the walleye resource of western Lake Erie be conserved by a combination of minimum size limit, quota, and fishing season regulations. Very few accidental captures in small-mesh nets should be tolerated; 5 or 10 percent of the total catch is far too high. Management policy should be reviewed annually in the light of current analyses based on samples of the existing populations.

We suggest that basic management policy be geared to stabilizing the fish System. The present policy of fishing heavily whatever species is currently abundant appears to increase the amplitude of those fluctuations that do occur, creating unstable and often economically inefficient conditions in the industry. The sudden occurrence of a very large year class of a valued species should be taken as a symptom of serious trouble in the ecosystem and not the source of glee that it appears to be under the current approach. Furthermore, it would not be proper management to increase quotas greatly with the occasional occurrence of large year classes. We make these suggestions to indicate that we have little faith in the sort of species management policies characteristic of the present approach in the Great Lakes. Our analysis is intended as a first step toward a more balanced, more rational, and we hope more successful systems approach to management of the Lake Erie fishery.

INTRODUCTION

The walleye [1] *(Stizostedion vitreum vitreum)* in Lake Erie and closely contiguous waters has supported a fishery for approximately 140 years. This fishery, which was concentrated in the western end of the lake, has been largely dominated, until recently, by Ohio commercial fishermen. Over the years the annual commercial catch from Lake Erie generally increased with many short-term fluctuations of modest amplitude (Figure 1). The Ontario commercial catch rose rapidly in the early 1950's and surpassed the combined Michigan and Ohio catches in 1956, when total landings of the walleye reached a very high and unprecedented peak. Catches then fell abruptly, in spite of intensive fishing efforts, and have not rebounded in strength since 1959.

There has been an extensive ice fishery by anglers in Ohio waters for many years which, when the species was abundant, was partly commercial and partly recreational. A moderately large summer recreational fishery for walleyes had developed in Ohio until the walleye "collapse" in 1957-58. Few Canadian anglers have shown interest in Lake Erie walleyes.

Many Americans and Canadians have shared, and continue to share, an interest and concern for the walleye of western Lake Erie. In failing to maintain a high population density, the walleye has joined an increasingly long list of Lake Erie species that once were, but no longer are, of major importance to the fishery.

Besides those who have, or have had, economic or recreational interests in western Lake Erie's walleye stock there is a group that see in the decline of the walleye another reflection of our lack of concern about humanity's impact on its biotic and abiotic environment. This group's concern is no less real than that of the commercial and sport fishermen.

The walleyes of western Lake Erie (including those in Lake St. Clair and the St. Clair and Detroit Rivers) are composed of a number of spawning groups which for most of the year are separate from walleye populations in eastern Lake Erie and southern Lake Huron. The fish in western Lake Erie do move periodically within the basin and into the in-flowing connecting waters, and large numbers of them cross the political boundaries separating

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[1] Common names of fish when first mentioned in this report are those recommended in the American Fisheries Society Special Publication No. 2, 1960; subsequent references to a species may vary somewhat within the limits of common usages in the Lake Erie area.

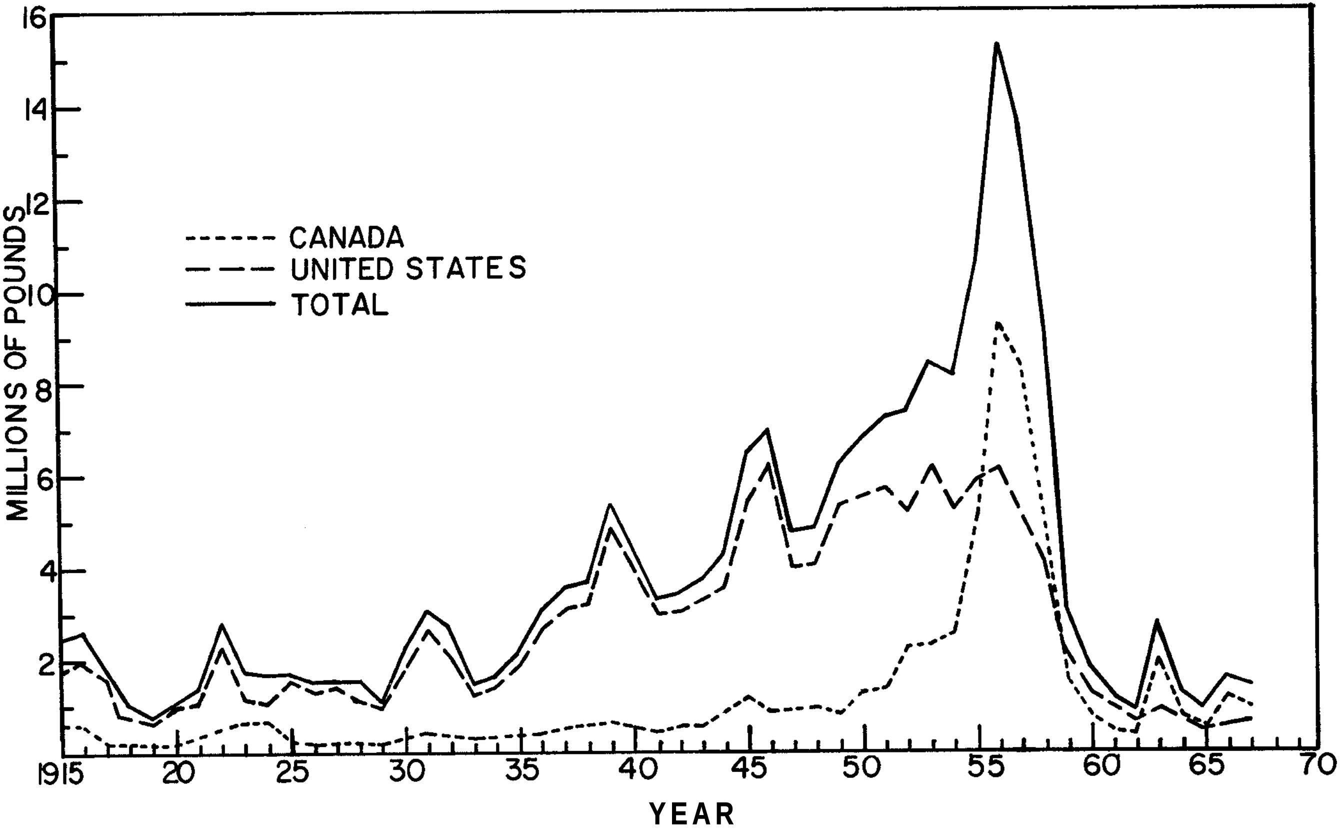

Figure 1. Commercial landings of walleyes from United States and Canadian waters of Lake Erie, 1915-67.

Michigan, Ohio, and Ontario. Hence, what happens to the walleye in one of these areas affects the interests of people in the other localities. Cooperation would seem to be in order but for nearly a century the agencies entrusted with managing this resource have disagreed on the action to be taken. The laws and regulations of one agency, when enforced at all, tended to work against those of another agency. Confusion has been widespread and some ill-will has arisen.

During recent decades many of the management decisions appear to have been based on short-run political considerations. Long-run considerations would require a firm base of ecological and economic information. Unfortunately, a satisfactory base has not yet been constructed. Much ecological information has been amassed but it has not yielded positive evidence on the proximate causes of the fluctuations of fish populations in western Lake Erie.

Fishery biologists no longer expect problems facing them to be either simple or to have simple solutions. Only occasionally in ecology has a problem been neatly identified, analyzed, and solved simply. Specifically, we have not found a simple explanation for the present problem and do not believe that one exists.

Our objectives in this study are the treatment of two questions. What are the factors that have limited and are now limiting the value of the walleye resource in western Lake Erie? How can one or more of these factors be managed to increase the value of the resource for contemporary and future users?

SOURCES OF INFORMATION

The scientific and management literature contains a large number of published and unpublished papers concerning the biology and ecology of the walleye and on fisheries that exploit it. Addison and Ryder's[2] bibliography on the *Stizostedion* species, which contains *over* 1,000 titles, has been particularly helpful. A number of current studies on walleyes in various parts of their range have also provided pertinent information. New information was submitted by W. D. Addison, W. J. Christie, J. L. Forney, N. R. Payne, L. L. Smith, and others (see Foreword).

Most studies relevant to the ecology of western Lake Erie have been conducted and reported by workers in United States agencies and institutions. Frequently, they also sampled Canadian waters so that we do have considerable information for the whole lake. There are, however, some limnological, biological, and other data collected by Canadian organizations. In the past decade, United States and Canadian fishery agencies have tried to complement each other's work. Ohio and the United States federal agencies have concentrated largely on the Western Basin and Ontario has worked more intensively in the Central and Eastern Basins.

An extensive general description of the environment and the organisms of western Lake Erie, based on earlier work, has been given by Langlois (1954). More recently, many analyses and reviews on limited topics concerning the physical dynamics, chemistry, pollutants, benthos, and microbiota of western Lake Erie have been published (e.g., Powers, Jones, Mundinger, and Ayers, 1960; Beeton, 1961; Hartley, 1961; Carr, 1962; Davis, 1964; Verduin, 1954, 1964; Carr and Hiltunen, 1965; Carr, Applegate, and Keller, 1965). No broad reviews nor general analyses have been published for the fish species. The most comprehensive, and also the most recent, analytic study of a number of fish species was Doan's (1942) monograph. These published papers and some unpublished data (e.g., reports of the University of Toronto's Great Lakes Institute) have been used to sketch the broad outlines of the factors in these waters that appear to be, directly and indirectly, of major significance to the walleye.

An extensive analysis entitled "Report on Commercial Fisher-

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[2] Addison, W. D. and R. A. Ryder. An indexed bibliography of North American *Stizostedion* species. Ontario Department of Lands and Forests. Unpublished manuscript.

ies Resources of the Lake Erie Basin," dated August, 1966, has been prepared by personnel of the U. S. Bureau of Commercial Fisheries (Anon., 1966). This report concentrates on the United States' part of the lake and its fishing industry but also includes much that is relevant to Canadian waters, for which there is not a comparable document.

Government agencies entrusted with the supervision of Great Lakes fisheries have maintained records of landings for commercially important species for the past century. A concise summary of annual landings has been presented by Baldwin and Saalfeld (1962) and summaries of more recent years' catches are also available from these authors. In the present study we required data on catches summarized in more detail, i.e., by months, fishing gear, and by the statistical districts defined by Smith, Beuttner, and Hile (1961). These data, for recent decades, were made available from the files of the cooperating agencies. A more detailed study was undertaken of the commercial catch statistics available for several selected years in an attempt to learn more precisely the seasonal and spatial distribution of the fish and the fishery. This study required a re-summarization of data from selected fishermen's reports.

Various important biological measurements can be obtained from the age, sex, and length-frequency distributions of the harvested animals. Samples of catches of walleyes in both Canadian and United States waters have been examined more or less routinely by biologists of the several research agencies to provide the data necessary for this purpose: These data were used in this study.

A number of mark-recapture experiments have been made in Lake Erie over the past 30 years to identify populations and trace their distributions in time and space. Some of the results have been reported by Doan and Edminster (1940), Ferguson and Cummins (1956), Ferguson (1957), and Wolfert (1963). A more recent analysis by R. G. Ferguson and A. J. Derksen has not yet been published.'

Biologists of the Ohio Division of Wildlife and the U. S. Bureau of Commercial Fisheries have, for a number of years, sampled the fish populations in United States waters of Lake Erie with experimental fishing gear. This work was carefully designed to provide reliable estimates of the relative abundance of the younger age groups of walleyes and other species. Ohio biologists have, in addition, fished standard, graded gangs of gill nets to provide

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[3] Ferguson, R. G. and A. J. Derksen. Migration of juvenile and adult walleye in Lake St. Clair, Lake Erie. and connecting waters. Ontario Department of Lands and Forests. Unpublished manuscript: 55 p.

data on older age groups and also on gear selectivity. Some supporting information has been provided by the Ontario Department of Lands and Forests.

Very large samples over a broad range of fish size are needed to obtain detailed estimates on the selectivity of gill nets from catches in standard gill net gangs. At the time of Ohio's netting activities, a sufficiently large size-range of walleyes was not present in Lake Erie to provide gill net selectivity estimates, but Ohio's data did permit adjustment of estimates from other sources. A large series of data on standard gill net catches of walleyes was made available by the Saskatchewan Department of Natural Resources[4] ; these data with information from the Ohio Division of Wildlife provided estimates of the selectivity of gill nets for walleyes.

Ohio began a study of the walleye spawning areas of western Lake Erie in 1960. Methods of sampling eggs with an egg pump were developed and spawning areas were located during the first several years of the study (Manz, 1964). In more recent years, various climatological and limnological conditions during the spawning season have been monitored by the Ohio Division of Wildlife and the U. S. Bureau of Commercial Fisheries in addition to the standardized sampling of eggs on Ohio's reefs. Reefs in Michigan and Ontario waters were also explored, but less intensively.

Walleye fry were hatched for many years in a number of hatcheries around Lake Erie. Various hatchery records and findings from special studies (e.g., Allbaugh and Manz, 1964) have been examined for corroborative information in various sections of this report.

Biologists, including the present authors, have always relied heavily on the information and ideas gained from repeated and extended discussions with fishermen. Their contributions and comments, though not always charitable or completely reliable, have been helpful.

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[4] These data were collected under the supervision of the late D. S. Rawson and F. M. Atton.

GENERAL ECOLOGY OF THE WALLEYE

Systematic status

Collette (1963), in a review of the Percidae, distinguished five species of *Stizostedion: S. vitreum* (walleye), *S. canadense (sauger),* and three European species, S. *lucioperca* (sander), *S. marina,* and S. volgensis. He made no reference to the blue pike as a distinct entity, and presumably classed it as a subspecies of S. *vitreum.* Collette reassigned the three European species to *Stizostedion* to comply with the taxonomists' law of priority, and considered North American and European forms to be congeneric, largely on the basis of morphological evidence. Svetovidov and Dorofeeva (1963) concurred with Collette's findings. The two groups are distinguished by rather marked ethological differences, e.g., at spawning.

Svetovidov and Dorofeeva (1963) suggested that the *Stizostedion* genus arose in Europe and that the ancestors of American Stizo*stedion* species evolved from a form similar to that of S. *marina.* The latter is restricted to brackish water, and the authors held that such a fish could have found its way along the edge of a hypothetical land or island bridge across the North Atlantic, sometime between the Oligocene and Pleistocene periods.

Range

Various writers have given the Great Lakes as the center of distribution of the walleye. Its limits are shown generally with those of the sauger *(Stizostedion* canadense) and the blue pike *(Stizostedion vitreum* glaucum) in Figure 2. The northern boundary for the walleye extends in an arc from the mainland near Anticosti Island in the Gulf of St. Lawrence (W. B. Scott, personal communication) to the southern edge of James Bay and thence northwestward to the southernmost arm of Great Bear Lake. Occasional wanderers are found farther north at the mouth of the Mackenzie River (L. Johnson, personal communication). The northern limit lies at approximately the 57° F. mean July isotherm (Ryder, Scott, and Crossman, 1964; W. D. Addison, personal communication; see Thomas, 1953, for isotherm data). Walleyes are found in the Liard River system and their westward limit extends

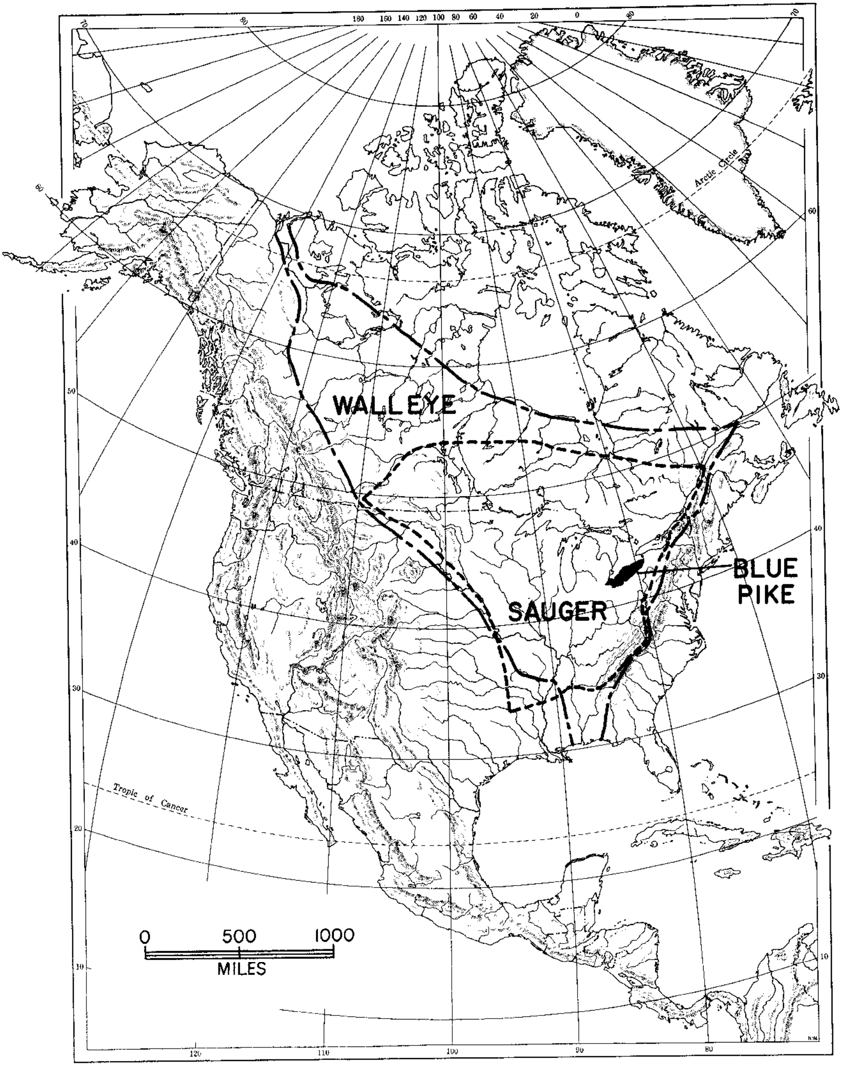

Figure 2. Distribution of walleyes, blue pike, and saugers (modified from Trautman, 1957). Eastern limit of the walleye does not include rivers flowing into the Atlantic in which the species may have been introduced. Blue pike in Lake Ontario may have been migrants from Lake Erie.

approximately along a line from there to Arkansas and Alabama where the species reaches its southernmost extension. The Allegheny Mountains form the eastern boundary, except for some rivers that flow into the Atlantic from Connecticut to North Carolina. Whether walleyes are indigenous to these rivers is uncertain because, unfortunately for the researcher, some of the earliest accounts of fish distribution postdate the earliest known introductions of *Stizostedion* forms (Milner, 1874b). However, we know of no records of introductions into Lake Erie or its tributaries before 1877, and believe that the walleye, blue pike, and sauger are indigenous there.

Habitat

The walleye, throughout its range, is a fish of larger streams and rivers and certain types of lakes. R. A. Ryder (unpublished data) has classified 43 Ontario lakes according to dominant commercial and game fish species and has attempted to determine the nature of the relationship between various limnological parameters and the ecologically dominant species. In 10 lakes classed as good "walleye-lake whitefish-northern pike lakes"[5] he found that turbidity ranged from 1.2 to 2.6 ppm (i.e., Jackson turbidity units), total alkalinity ranged from 22 to 60 ppm, and total dissolved solids from 47 to 83 ppm. These measurements describe lakes of intermediate turbidity and fertility that we might term mesotrophic . He found more turbid and more fertile lakes to be dominated by warm-water species such as centrarchids and less turbid, less fertile lakes by salmonids.

Moyle (1954) related the chemistry of Minnesota surface waters to fish associations and found that walleye habitats, although exhibiting a considerable range in total dissolved solids (with carbonates predominating) were generally associated with the following chemical characteristics: total phosphorus, 0.04 ppm; total nitrogen, 0.4 ppm; chloride ion, 1.0 ppm; and, sulphate ion, 2.1 ppm. In Minnesota, good "walleye waters" are typically in areas of coniferous forest. Within its typical range, in suitable lakes, the walleye usually produces a sizeable year class each year. In more fertile waters, like those of southern Minnesota, introduced walleyes showed only sporadic successful reproduction. Walleyes introduced in lakes of low fertility in northeast Minnesota grow slowly and have, in a number of them, apparently displaced lake trout *(Salvelinus namaycush)* populations.

That high levels of total dissolved solids in themselves do not limit nor preclude successful walleye populations can be deduced

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[5] *S. v. vitreum-Coregonus clupeaformis--Esox lucius*

from Rawson's (1946) finding that introduced walleyes thrived in a Saskatchewan lake with total dissolved solids of about 15,000 ppm (mostly sodium and magnesium sulphates).

From the above data, and much similar information scattered through the literature, we infer that the walleye can be expected to do well in mesotrophic waters and less well in oligotrophic, early eutrophic, and advanced eutrophic environments. In addition, we judge from the literature and from data in the files of agencies cooperating in this study that the sauger prefers somewhat more turbid waters though of similar trophic state, and that the blue pike prefers somewhat colder waters than does the walleye.

Ryder et al. (1964) and R. A. Ryder (unpublished data) have found that the depth distribution of the walleye, in "walleye waters", is determined more by light intensity than by any other factor, unless oxygen is deficient in deeper waters. He agrees, from extensive field observations, with Moore (1944) who stated that the adult walleye's eye is adapted to dim-light conditions and has not developed adequate mechanisms to compensate for large differences in light intensity. In consequence, larger walleyes generally remain in turbid water (often associated with currents) during hours of sunlight, or move to deeper waters, or enter shady areas under rocks, logs, or weeds (Kirtland, 1838; Carlander and Cleary, 1949; Whitney, 1958).

J. L. Forney (personal communication) has found that at an early stage of development walleyes have a strong, positive phototropic response. From the time they hatch until they reach a length of about 1.5 in., they can be attracted to a light source at night. Obviously, they are not sufficiently averse to light to prevent their concentration near the surface when pelagic and along the shore in shallow water in early summer.

The walleye apparently relies largely on sight to find its prey. Efficient sight feeding, especially for a large fish seeking relatively large, mobile prey, requires sufficient water clarity to discern the prey at some distance. Thus, if turbidity is excessive, we would expect the walleye to be an ineffective predator. Although the walleye appears to be a sight feeder, it is readily caught at night on bait or lures; some anglers on Oneida Lake, New York, claim a dark night, when there is no moonlight, provides the best fishing (J. L. Forney, personal communication). This and other evidence implies a partial reliance on some, or all, of the senses of sound, taste, or smell for feeding. If sight is the major sense used in the capture of prey, then the walleye must strike a balance between sufficient turbidity to dim the sun's light during the day and sufficient water clarity to find its mobile prey at sunrise and sunset.

The walleye reportedly prefers a temperature of about 70 to 72° F. in summer (Ferguson, 1958). Some older, larger walleyes migrate out of the epilimnion during the summer and into depths of 80 to 90 ft. Wakeham and Rathbun (1897) found this behavior in eastern Lake Erie; Van Oosten, Hile, and Jobes (1946) noted it in Lake Michigan and Payne (MS, 1964) observed it in Lake Ontario. Temperatures at these depths probably range in the low 50's (°F.). Water temperatures in summer in McVicar Arm of Great Bear Lake, the location of one of the northernmost known populations of walleyes, rise only to about 57° F. (L. Johnson, personal communication). Walleyes are found in several large rivers in Illinois (Rock River, Mississippi River) and the rather sluggish Illinois-Mississippi Feeder and Main Canals, but in no Illinois lakes (L. L. Rock, personal communication). Some resident populations in the rivers tolerate water temperatures as high as the mid-80's (°F.) for extended periods. Rock believes that temperature restricts the walleye from many waters in Illinois, but has found no evidence of summer "kills" due to high temperature. It appears likely, from all available information, that light intensity is a more important factor in determining depths selected by the walleye in summer than is water temperature (Ontario data). We judge from these observations that the walleye is a eurythermic animal which, in favorable light conditions, prefers temperatures of 70-72° F. at our latitude.

Although we have no direct data on lethal limits of combinations of high temperatures and low oxygen concentrations for the North American *Stizostedion* species, we judge from data on environmental conditions where they thrive (or once thrived) that the blue pike prefers lower temperatures than the walleye. Since the range of the sauger does not extend as far north as the walleye, but extends somewhat farther to the southwest, we suspect that it is less tolerant of low temperatures and somewhat more tolerant of high temperatures than the walleye. On the other hand, turbidity and sensitivity to light may be important factors for all *Stizostedion* species.

Scuba divers who have inspected the reefs of western Lake Erie report that walleyes may be seen during daylight lying motionless on the bottom. Many similar observations have been made in other lakes by biologists using Scuba gear (R. A. Ryder, unpublished data; also personal communications: W. MacGregor, 1966, and W. D. Addison, 1967). Observers report also that other walleyes may be seen swimming at such times, either in deeper waters or in turbid, shallow waters. Most of the percid species (e.g., the darters) regularly touch bottom for most of the day. The yellow perch *(Perca flavescens)* may be the nearest to being a pelagic percid, but here, too, inactive periods occur at night with the perch resting on the bottom (Scott, 1955; also unpublished Ontario data). Certain stages of the *young* of *Perca* and *Stizostedion* are pelagic. Among yellow perch, the pelagic habit may extend well through the first summer (Ontario data) but not for as long as does that of the walleye (J. L. Forney, unpublished data). We deduce from these findings and other references that older percids have, in general, a daily inactive period that brings them into contact with the bottom. (This also appears to be true for centrarchids, ictalurids, catostomids, and some cyprinids, salmonids, and others. In fact, only a few freshwater fish species are completely pelagic).

Experienced commercial and sport fishermen expect to find walleyes concentrated on, or over, clean hard bottom, i.e., rocky reefs, hardpan, or clean sand and at the edge of weed beds. Reefs are presumably good feeding places due to the presence of emerging insects and small fish. We suggest that the daily "resting requirements" of walleyes may also tend to limit them to such areas. Their requirement of a relatively high oxygen concentration, as inferred above, prevents them from resting on muddy or silty areas with high organic content where oxygen concentrations tend to be low during periods when currents or vertical mixing are slight.

J. L. Forney (personal communication) stated that walleyes in Oneida Lake tend to concentrate over areas of hard bottom but that they are not limited to this type of bottom if oxygen conditions are reasonably favorable elsewhere. The adult population apparently moves laterally from relatively shallow water (10-20 ft.) in May and June to progressively deeper water during the summer. By middle or late August, significant numbers of walleyes can be taken by trawling at 30-40 ft. over mud bottom. If forced out of deeper waters by low oxygen after temporary thermal and chemical stratification, walleyes reappear in these areas within 2 to 3 weeks after the oxygen concentration again becomes adequate.

Forney's observations are based on trawling, which in Oneida Lake is limited to a few sand bottom areas at depths of 15-20 ft. and extensive areas of muck bottom at depths of over 25 ft. Shoals are not sampled by trawl, hence it is impossible to determine directly what proportion of the population might be resting on mud bottom. On the basis of the area swept by Forney's trawl and the catches he made, it would appear that significant numbers are resting over mud bottom. The average catch in late summer and fall is about 20 age IV and older walleyes in a haul covering approximately 3 acres; population density in the lake has ranged from 15-20 fish per acre during the years when this trawling has been conducted.

In summary, we believe that the walleye is most successful in mesotrophic waters and not very tolerant of either oligotrophic or advanced eutrophic conditions. More particularly, we expect to find walleyes, at least in summer, in waters with a turbidity between about 1 and 3 ppm (Secchi disc reading roughly 4 to 10 ft.), a depth of at least 30 ft. (if the water is fairly transparent), a temperature between 60 and 80° F., and a bottom that contains areas of clean rock or sand.

Reproduction

Walleyes spawn commonly over rock, rubble, or gravel in streams, shallow offshore reefs, or along shorelines of lakes (Eschmeyer, 1950). Some populations spawn over vegetation in flooded areas (Nevin, 1900; Schumann, 1964). Still, the absence of suitable spawning areas seems to be a major factor preventing walleyes from establishing themselves in some eutrophic lakes (Moyle, 1954).

We know of no species of fish that regularly lays "unprotected" eggs on an undisturbed mud bottom. The eggs of some species (e.g., deepwater chubs), although laid on such a bottom, are protected from extensive contact with the bottom because they retain loose contact with each other and are semi-buoyant (S. H. Smith, personal communication). Lake-dwelling species have developed migratory and homing behavior, or other complex physiological mechanisms or behavior patterns, that effectively prevent deposition of unprotected eggs on a mud-water interface. We can infer, therefore, that the latter must generally be unsuitable for egg development. Colby and Smith (1967) found that oxygen concentrations are likely to sink to low levels very near the mud-water interface, and that hydrogen sulphide concentrations are apt to be high.

The evidence just reviewed suggests that if stream, reef, or shore areas become enriched and begin to take on some of the faunal and floral characteristics of a mud-water interface, we would expect hatching success to deteriorate in these locations.

Walleye eggs are adhesive for some hours after spawning and then lose their adhesiveness (Leach, 1928; Nelson, Hines, and Beckman, 1965). If deposited on rocky or gravelly areas, they may adhere to the rocks for a short time, but ultimately drop between them. If these cracks and crevices have become partly filled with mud and associated organisms, the settling eggs would, in effect, land on a mud bottom. Also, if the interstices are partly filled, there would be a greater likelihood of eggs being found by egg-eating fish or other organisms, or washed out of the crevices onto an even less hospitable bottom.

Walleyes have a high fecundity; various studies have shown between 30,000 and 300,000 or more eggs per female, depending partly on female size and partly on other factors (Carlander, 1950a). As many as 612,000 eggs have been found in a large walleye from western Lake Erie (D. R. Wolfert, unpublished data). That this species lays such a large number of eggs (much larger than most freshwater species) indicates that under normal circumstances, even in good "walleye waters," a very large proportion of eggs cannot be expected to survive through the fry stage. The question of the percentage of eggs deposited naturally that were fertilized and hatched has puzzled biologists and fish culturists of past decades. Baker and Manz (1967) found, over a 7-year period, that between 19 and 49 percent of large numbers of eggs taken from reefs in western Lake Erie had live, developing embryos.

Weather conditions may be the critical factor affecting survival at this early life-stage. Winds that generate strong currents or seiches would tend to sweep eggs from reefs and shores and deposit them in less suitable places. Freshets would scour stream beds or deposit silt on them. Fluctuating temperatures would tend to disrupt spawning in the sense that the fish might spawn intermittently over a period of weeks instead of over a much shorter interval if temperature rose steadily. Schumann (1964) reported that during a cold spring, following a warm initial burst, many walleyes failed to spawn and that many eggs spawned late in the season were sterile, apparently because they were physiologically too old.

Baker and Manz (1967) have found an inverse relationship between relative abundance of young-of-the-year walleyes in late summer and the length of time required for walleye eggs to hatch. They also found no discernible relation between the success of the "hatch" and the relative abundance of eggs, or the percentage of them viable. It appears, however, that if the water warms rapidly after most spawning is completed, the number of fingerlings produced is above average. Whether temperature is, in fact, the immediate factor, or whether it is some combination of correlated factors (as we might suspect), is not known. Payne (MS, 1964) found some evidence that stronger year classes of walleyes tend to arise during warmer than average spawning seasons. Other workers have discovered no comparable relationship (Carlander, 1945; Doan, 1942).

Predation on young

Aside from the apparent vulnerability of walleye egg and yolk-sac stages to events correlated with storms, temperature, and eutrophic conditions, the behavior of the fry after the yolk has been absorbed adds to the problems of survival. The fry rise to the surface where they remain for several weeks feeding upon plankton and being preyed upon themselves by other fish (Forney, 1966).

If piscivores of the right size to catch fry efficiently are abundant in the surface waters, we would expect a hatch of walleye fry to be decimated. No detailed studies have been reported on the predation of larger fish on walleye fry. Fry of no other species in “walleye waters” are likely to be large enough to be predators when the walleye fry are pelagic (usually in May and June). Furthermore, the largest pelagic predator fish (older walleyes) are probably ineffective in capturing small fry. We suspect, therefore, that it is the yearlings and older fish of species like the yellow perch, white bass (Roccus chrysops), alewife *(Alosa pseudoharengus),* and American *smelt* (Osmerus *mordax)* that are the effective predators on the pelagic young of the walleye.

J. L. Forney (personal communication) suspects that predation on walleye fry is most serious in streams or immediately adjacent to shoals where walleyes spawn. It is only in these areas that fry would be sufficiently dense to attract predators and where predators are likely to feed selectively on fry. Young perch (ages I and II) enter the lower sections of streams flowing into Oneida Lake during the spring. In one of these tributaries, Scriba Creek, yellow perch have been found “stuffed" with walleye fry. This situation may be abnormal, because the constant loss of fry from the Constantia Hatchery, located on the stream, places relatively large numbers of fry in the creek. The low density of fry after they have dispersed in the lake may afford some protection from predation, judging from Ivlev’s (1961) studies of the effect of food density on selection.

Food, feeding habits, and predatory interactions

Hohn (1966) found that diatoms were the first food of pelagic walleye fry in western Lake Erie. Smith and Moyle (1945) observed that rotifers were the most important early food of fry in rearing ponds. On the other hand, Houde (1967) found that large zooplankters, particularly copepods, were the initial food source of walleyes in Oneida Lake. Although rotifers. were abundant in plankton samples from Oneida Lake, only one was found in a walleye stomach during a 3-year study-which suggests some food selectivity at an early stage of development. Rogowski and Tesch (1960) found that sander did not eat rotifers although these were common zooplankters available to them.

Some European workers hold that weather conditions during and shortly after the spawning seasons are critical for fish because weather largely determines whether suitable food organisms will be available when needed (see e.g., Tesch, 1962; Einsele, 1965). So far as we know, no direct evidence has been advanced that suitable food is sometimes unavailable for walleye fry.

Whether walleyes at any life-stage have a pronounced preference scale of prey species is debatable. Apparently no one has examined the problem critically, taking into account, among other factors, the relative sizes of predator and prey. Wolfert (1966), in a study of the food habits of young-of-the-year walleyes in Lake Erie, found evidence that they selected a higher proportion of small, pelagic cyprinids than yellow perch of equal size. Soft-rayed fish including emerald shiner *(Notropis atherinoides),* spottail shiner *(Notropis hudsonius),* and alewife appear to be preferred where they are available, but other species are often taken (see Doan, 1942; Moyle, 1949; Rawson, 1957; Payne, MS, 1964; Wolfert, 1966). In short, the walleye would be likely to starve only in those waters where few mobile organisms of intermediate size are available.

The growth of walleyes in some lakes of Northern Ontario is very slow. Unpublished data collected by R. A. Ryder show that very few small cyprinids, percids, salmonids, etc., can be caught in such lakes. Here, presumably, availability of food is the limiting factor. Forney (1965) has found that slow growth of the walleyes in Oneida Lake in some years can be related to a low abundance of prey of suitable size. In such years, Forney has found that relatively few perch survive their first year, apparently falling prey to the walleyes in that-brief period. Tesch (1965) has found that the sander and European perch *(Perca fluviatilis)* have an interaction similar to that of the walleye and yellow perch in North America. If the sander manages to maintain adequate year classes year after year, the perch population suffers, and vice versa. Moyle, Kuehn, and Burrows (1950) noted that Minnesota lakes which were suitable limnologically for walleyes had sparse populations where yellow perch were abundant. Yellow perch of various life stages may be heavily preyed upon by walleyes of corresponding older life stages thus ruling out direct competition for food as a reasonable general hypothesis for such occurrences (Moyle, 1949). We would expect, however, that predation by very numerous small perch upon walleye fry would limit effectively the abundance of walleyes.

American smelt and walleyes occur together in few waters. In the Great Lakes these populations have not come together until recent decades. Van Oosten (1947) found some evidence that smelt had acted to limit the success of year classes of lake herring *(Coregonus artedii),* lake whitefish *(Coregonus clupeaformis)* and "perhaps walleye" in Green Bay of Lake Michigan.

Cannibalism may also occur under certain circumstances. J. L. Forney (personal communication) has found evidence consistent with the hypothesis (though not conclusively so) that dense populations of older walleyes prey on young-of-the-year walleyes during their first winter, when both age groups occupy similar environments. A self-limiting mechanism of this type would certainly act to reduce, if not regulate, abundance.

Where walleyes grow at a rate near their physiological maximum for the species, we believe that food is abundant and do not expect to find either significant intraspecific competition or intensive predation by adults on young. A growth rate near its physiological limit can be expected where a relatively small number of a species is introduced for the first time into suitable waters or when the numbers in an established population become low. Stroud (1949) has described the rapid growth of walleyes following such an introduction. The growth rates of walleyes in western Lake Erie in recent years have surpassed those reported by Stroud. In fact, no more rapid rates than these have ever been recorded.

From the above observation, the walleye appears to be a rather generalized predator upon organisms occupying all habitats within their common environment.

Populations, stocks, spawning migrations, and spawning behavior

Where walleye distribution and movements have been studied carefully by mark-recapture methods it has usually been found that larger waters contain more than one population or stock. In very large waters, these populations may remain spatially isolated except for the occasional wandering member. Thus, it can be demonstrated that Lake Huron and Georgian Bay contain (or once contained) largely discrete populations centered as follows: Southern Lake Huron; Saginaw Bay; Thirty Thousand Island Region (comprising a number of stocks); and, the North Channel (Leach, 1963; Payne, 1966; R. M. Christie, personal communication). Lakes Erie, Michigan, Ontario, and Superior (Ryder, 1968) each also have (or had) a number of relatively discrete populations.

Large populations of walleyes, even if localized in a single bay or smaller lake, have been found to be heterogeneous with respect to their seasonal distribution and movement patterns. Several stocks, which spawn during the spring in widely separated areas in western Lake Erie, Lake St. Clair, and interconnecting waters and tributaries intermix at other seasons. Studies in Green Bay of Lake Michigan and elsewhere confirm further that although individual members of different stocks may mingle more or less freely in summer and early autumn in a given locale, they segregate at spawning time and home to a particular spawning ground (Anon., 1966; Crowe, 1962; Crowe, Karvelis, and Joeris, 1963; Forney, 1963; Payne, MS, 1964; and others). All studies have shown that relatively few walleyes tagged in one spawning area in one year are recaptured in another area in a following year except where spawning grounds are within a few miles of each other. Whether these errant walleyes actually spawn on another reef or were simply caught during an erratic migration to their own spawning grounds is not known. A stronger drive toward schooling and spawning than to the continuation of migration may lead to "school-trapping" of some individual walleyes.

The spawning behavior of walleyes has been described a number of times (Eschmeyer, 1950; Schumann, 1964; Baker and Manz, 1967; and others). Often one female is escorted by a number of males during the emission of sex products. The act of emission may occur some distance off the bottom, and the eggs settle gradually to the rubble, rock, or vegetation below. The fact that a number of males escort one female may be a behavioral adaptation to compensate for a relatively low likelihood of fertilization due to a short-lived viability of either the egg or the sperm. Stranahan (1900) stated that walleye milt dies in 2 minutes and eggs cannot be impregnated after 6 minutes exposure to water. If this is so, simultaneous spawning by a larger number of walleyes over a small area should increase the probability of fertilization.

Hybridization and introgression among *Stizostedion* species

The recent reduction in abundance of walleyes in Lake Erie followed the disintegration of the population of blue pike. Both of these events attracted a great deal of attention. Less well noted was the more gradual demise of the related sauger, once very abundant in waters along the south shore and now almost totally absent from the lake. Were these occurrences independent of each other? We doubt that they were. If not, then how were they related? We suggest that all three species suffered from changes in various aspects of their environment, where "environment" includes changes in fish populations and the activities of predatory man. Furthermore, an additional factor of a different kind viz., introgression, conceivably was responsible for the final disappearance of the blue pike and possibly the sauger.

Man's direct or indirect effects on other species and their environments have not infrequently led to the destruction of reproductive isolating mechanisms between spawning runs, varieties, or even sibling species, with consequent hybridization (Stebbins, 1966). Most hybrids, if they do not die at a young age, are wholly or partly sterile. Furthermore, the genotypes found in subsequent generations of the relatively fertile hybrids are usually highly heterozygous and consequently will not breed true. Where hybrids are less numerous than the parent species, most will breed with one or other parent forms-thus leading to introgression. If these crosses continue to be wholly or partly sterile, the total number of progeny of a population (pure parents plus hybrids) will, on the average, be lower than before hybridization and subsequent introgression occurred.

A breakdown of reproductive isolating mechanisms between two or more species is usually to the disadvantage of those species in terms of their combined abundance in the ecosystem. Spectacular instances of man-induced changes in populations of some forms of coregonids and salmonids have been described by **Svärdson** (1961, 1965). We believe that introgression among the *Stizostedion* species is a distinct possibility (Regier, 1968) and could explain the disappearance of the blue pike and sauger in Lake Erie. The latter possibility is explored further in a subsequent section dealing specifically with the walleye in western Lake Erie.

Natural mortality

Walleyes over 10 years old are not uncommon in unexploited populations in Canada's northern waters (R. A. Ryder, unpublished data). Since relatively few yearlings are generally present in these waters we can infer that yearling and older walleyes have a relatively low natural mortality. In view of their high fecundity it follows that the first year mortality (egg to yearling) is very high. In some waters (e.g., eastern Lake Erie) almost all of this initial mortality appears to occur at the egg and fry stage; in others (e.g., Oneida Lake) an appreciable amount may occur during the first winter depending upon the relative density of adult walleyes.

Natural mortality has been estimated for relatively few walleye populations. The following estimates have been obtained for adult walleye populations that are subject to fairly intensive sport fisheries: 5 percent (Olson, 1958); 0 to 9 percent for various years (Churchill, 1961); 6 percent mean for a series of years (Forney, 1967). Each of the estimates have been corrected for concomitant fishing mortality by the standard method of Ricker (1958, p. 25).

Payne (1966) estimated annual natural mortality at 33 percent which was similar to an average of those estimates derived by Ryder (1968). Both men worked with more northerly populations that were exploited less intensively than those mentioned in the preceding paragraph.

Walleyes apparently are not particularly susceptible to severe epizootics; we know of no account of mass deaths in populations of walleyes due to disease or parasite infections. Some parasites are regularly found in their intestinal tract, and viral lymphocystis protuberances are seen in some populations in spring; these do not appear, however, to be debilitating (Hile, 1954; Ryder, 1961; Wolfert, Applegate, and Allison, 1967).

The walleye seems, from what we know about it generally, to be well qualified as a dominant predator to help stabilize various populations of larger organisms in an aquatic ecosystem. It tends not to become seriously crowded, at least under moderate exploitation, although Van Oosten and Deason (1957) have described a case of a stunted walleye population that was exploited only very lightly. It is long-lived. It is a general predator. It grows rapidly and reproduces at a fairly young age when food is abundant. It feeds actively in winter. It is not markedly sensitive to environmental fluctuations. It tolerates a wide range of environmental conditions.

HISTORY OF FISH AND FISHING IN LAKE ERIE

We consider it axiomatic that fishing, no matter how extensive, has an effect on the fish and their ecosystem-the greater the intensity of fishing the greater the effect on the ecosystem. To argue against this is to deny causality in nature. Therefore, we must examine the history of fishing if we hope to gain a broad insight into the ecosystem and the catch fluctuations of past years.

Fishing before 1900

The Indians living near the shores of Lake Erie utilized fish as one of their staple foods and used a variety of primitive methods to capture them (Rostlund, 1952). The Indians were relatively few and trade was limited, thus their impact on the ecosystem must have been small.

The first European settlers used fish to supplement other sources of food. They took fish when they were plentiful inshore, usually during spawning seasons, by crude and simple methods: spears, brush weirs, baskets, simple seines, or hook and line.

A hook and line commercial fishery began in eastern Lake Erie with the settlement of Presque Isle, Pennsylvania, in 1795. The first regular, commercial fishery in western Lake Erie began about 18 15 with seining in Maumee Bay and the Maumee River. Whitefish, the most desired fish in those times, entered the Bay but only in small numbers, and sauger, walleye, and smallmouth bass *(Micropterus dolomieui)* were the principal species caught in 1815 and throughout much of the 19th century (Klippart, 1877; Smith and Snell, 1891). Fishermen at Ecorse on the Detroit River began seining for whitefish about 1830 and seines were used almost exclusively in the Detroit River from then until the whitefish disappeared from these grounds about 1920. Lake herring could also be taken in large numbers in the Detroit River until about 1920. If any commercial fishing existed in the Canadian waters of western Lake Erie before 1850, it must have been restricted to a few seiners on the Detroit River or inshore areas of the lake.

Seining spread gradually from the bays to the shores of the lake proper in Michigan and Ohio and reached its peak in number of units and catch between 1850 and 1860. Seines were then gradually, but only partially, superseded by pound nets and gill nets. In Ontario, seines were used in the Detroit River after about 1850 and in Long Point Bay (starting date unknown). They were not fished in the lake proper until 1901 and were never a major gear there.

Pound nets were first set about 1850 in Maumee and Sandusky Bays and in Presque Isle Bay in 1852. These so-called bay nets were set inshore in shallow water and at first did not have tunnels into the hearts to reduce escapement (True, 1887). They were constructed from remnants of seines and were tended by small rowboat. Tunnels were introduced during the next 2 decades and larger nets were built to set in deeper water, requiring construction of pile-driving and stake-pulling equipment, as well as bigger boats.

As pound nets increased, strings of them extending into the lake intercepted fish that would normally have gone to the beach seiners with the result that seining became less profitable than pound netting. The currents and the nature of the bottom deposits off the Maumee River, except near its mouth, and those of the Detroit River made these localities unsuitable for pound nets; continuing large concentrations of spawning fish were exploited by seiners in these waters. Pound nets were introduced in Ontario waters, along shore and off Pelee Island, in 1869. Fifty were licensed by 1885, but only 62 were in use by 1900.

There was apparently some ill-will on the part of seiners towards the pound netters who had pre-empted the fishery. There were, however, compensating factors, according to Milner (1874a), who pointed out that the decrease in the number of lake sturgeon *(Acipenser fulvescens)* in Ohio waters had several times been advanced as an argument in favor of the pound net. The destruction of the sturgeon, asserted to be an extensive spawn-eater and damaging to seines, more than compensated for the numbers of whitefish taken.

Sturgeon, very abundant in early years, were not marketed until about 1860. They were then smoked in increasing numbers and sold originally as “smoked halibut.” By-products of the sturgeon, caviar and isinglass, were also exported to Europe. Sturgeon were no longer abundant in western Lake Erie by 1885, but were still taken in large numbers farther east (Smith and Snell, 1891).

Gill nets first were used commercially in 1852 in eastern Lake Erie off Dunkirk, New York (Meehan, 1897). Early nets were heavy and of coarse, cotton twine knit by the wives and daughters of fishermen. Linen was introduced about 1858. By 1870, the nets were generally of finer and stronger cotton or linen and were usually purchased “ready-made.” Lake trout and whitefish were caught first in 6-in. mesh (all gill net dimensions given in this report are “stretched measure”). Later, the whitefish were taken with 4-1/4 to 4-1/2 in. mesh and lake herring with 3-1/8 to 3-1/4 in. mesh. Since herring and whitefish shoaled together, many young whitefish were killed by herring nets, much to the consternation of western pound netters, who detected a decrease in availability of whitefish by 1880 (True, 1887).

The use of gill nets spread gradually westward, reaching Cleveland and western Lake Erie about 1877. They were used for a number of years exclusively for taking lake whitefish in autumn near the Bass Islands, Kelleys Island, and on Niagara Reef. Smaller mesh gill nets were first used in 1884 in the same area but near the south shore for catching saugers; these fish were taken in sufficient numbers to glut the market (Smith and Snell, 1891). Herring and whitefish were not abundant, except occasionally, along the south shore from Cleveland westward. We surmise that the inshore water here was too warm or turbid for these species. Gill nets were first used in the Island Region (Bass Islands, Kelleys Island, Pelee Island) for taking herring about 1888 (Langlois and Langlois, 1948). In the Ontario waters, gill nets were tried in small numbers (less than 5,000 yds.) occasionally between 1869 and 1899, but were not used regularly there until after 1900.

Trap nets were introduced about 1890 in western Lake Erie (Langlois and Langlois, 1948). They were more flexible and manageable than pound nets and permitted more efficient fisheries in deeper water or where sand and mud was not sufficiently deep to hold pound net stakes. Eventually some with steel chain-link bottoms were even tried in rocky places (M. Hosko, personal communication).

The improvement in transportation systems (road, rail, lake, and canal) and the increase in human population raised the demand for fish. Freezing fish, done on a small scale under patent at Sandusky since about 1855, increased markedly in 1869 (Keyes, 1894). Steamboats were introduced about 1880 at Sandusky to pull pound net boats to their gear and collect fish from gill netters. Gill netters rapidly turned to larger steam-powered vessels. Concurrently, lake herring became more available in the Central Basin. **We suggest that the higher catch of herring could have been due** in part to less predation by sturgeon on their eggs, in part to less predation on older herring following the collapse of the lake trout population in the Eastern Basin, and, in part to increasing markets for this species since 1870. There were also indications that saugers became more available along the south shore from Toledo to Cleveland as did the blue pike from Sandusky eastwards. We think the greater availability of these species was because of increased abundance due to increased turbidity and fertility that, in turn, was caused by erosion from land clearing and cultivation and fertilization from manures and domestic wastes. That waters along the south shore were more fertile than those along the north shore of the Central Basin can be inferred from an observation by Wakeham and Rathbun (1897) who stated that nets could not be left in the waters off the south shore in June and July due to destructive "vegetable slime" forming on them, but that this was not then a problem along the north shore.

All of these factors contributed to the entry of the so-called coarse fish, e.g., herring, saugers, and blue pike in large numbers into the United States fishery in the 1880's. Previously these species had not been fished intensively due to low prices (Keyes, 1894). Ontario's lake herring fishery also expanded rapidly at this time and blue pike were taken in moderate numbers, but saugers apparently were caught only infrequently. Most of the Ontario catch came from pound nets; few gill nets were reported in use.

In addition to the pound nets, fyke nets, seines, and gill nets, an extensive trot-line fishery began about 1850 in the Ohio waters from Toledo to Cleveland but particularly in the Western Basin. The species taken in this fishery were bullheads and catfish *(Ictalurus* spp.).

Large numbers of fyke nets were set in the shallowest areas of Maumee Bay, Sandusky Bay, and various inshore areas for smallmouth bass, walleyes, catfish, etc. These nets were very numerous in the 1880's. Fyke netting and seining could be done under the ice and these operations, together with spearing and hook-and-line fishing, provided fish in mid-winter when more efficient gears could not be used.

The trend in fishing in Ohio and Michigan during the 1880's was toward bigger pound nets set in increasingly long lines into the deeper waters of western Lake Erie. More and larger steamships were used. Gill netters out of Sandusky were most numerous in the Central Basin fishing for saugers, lake herring, and lake whitefish. Whitefish spawning grounds in the Island Region were fished heavily by gill netters in the autumn (Smith and Snell, 1891). Large numbers of undersized fish caught in small mesh nets set in the 1890's were sold to a fertilizer factory in Sandusky, Ohio. Table 1 shows amounts of gear used in western Lake Erie during 1879 and 1885. The pre-eminent position of Ohio is apparent. Its main fishing port, Sandusky, was at this time referred to as the "freshwater fish capital of the world."

The catches of the most valuable species, whitefish and herring, in United States waters of Lake Erie reached their maximum during the 1880's. During this period Canadian landings were less than 10 percent of the United States landings. Canadian catches of these species did not "peak" until 2 or 3 decades later (Baldwin and Saalfeld, 1962). The Ontario fishermen of western Lake Erie

Table 1. Major gears fished in western Lake Erie in 1879 and 1885.

Year	Political division	Gill nets (1,000 yds.)	Pound nets (number)	Fyke nets (number)	Seines (number)	Hooks (1,000's)
1879	Michigan [1]	0	182	30	5	?
	Ohio[1,3]	15	604	785	13	8
	Ontario[2]	5	23	0	0	0
1885	Michigan[4]	0	204	43	4	30
	Ohio[4,6]	510[7]	437	1,008	55	48
	Ontario[5]	0	50	0	0	0

1 Data from True (1887).

2 Data from Ann. Rept., Canada Dept. Marine and Fisheries.

[3] Includes data from Sandusky Bay fisheries for which data are not listed separately; these fisheries may account for about 40 percent of the gear.

[4] Data from Smith and Snell (1891).

[5] Data from Ann. Rept., Canada Dept. Marine and Fisheries.

6 Includes Sandusky Bay in which "nearly a thousand fyke nets and small pound-nets are fished" (Smith and Snell, 1891: p. 265).

7 Based on average net length of about 80 yds. (Smith and Snell, 1891: p. 255).

disposed of almost all of their catch in the United States during the 1890's. Because of the greater distance from markets only the currently most valued species were sought, i.e., whitefish and herring. Market demand was often very limited, regulations were strictly enforced, and the Ontario fishery did not expand nearly as rapidly as that of Ohio.

The annual reports of the Ohio Fish and Game Commission for this period are eloquent in their concern for the welfare of the fishing industry. For example, the report for 1894 states as follows:

"The Lake Erie fisheries in a commercial sense are of more importance than any other with which your Commission has to deal. From the year 1882, the supply of fish in Lake Erie increased steadily, until about the year 1890."

"Since that time there has been a steady decrease in the catch of the most valuable fish of the lake. From time to time . . . the Commission has contended for laws . . . but as regularly as the General Assembly convened, the fishermen and dealers from one end of the lake to the other, tried to defeat any and all bills offered or recommended by the Commission."

This sequence of concern, recommended action, and obstructionism continued throughout the ensuing decade, until 1906 when the Commission reported:

"It has been the constant aim of the present Commission to have laws enacted to preserve the great food supply of the lake and at the last session of the legislature, it succeeded in having passed several laws that are in the opinion of the best fishermen on the lakes, good laws, and they are beginning to realize that the efforts of the Commission are for the common good and are working with instead of *against* the Commission for the proper enforcement of the law."

Artificial propagation and regulation of the fishery

The decreased availability of whitefish about 1870 in the American waters of western Lake Erie and the Detroit and St. Clair Rivers stimulated local interest in artificial propagation that had been pioneered in Europe some decades earlier. A number of private fish hatcheries sprang up in the area. Dr. T. Garlach had built one about 1850 at Cleveland but he had concerned himself largely with the hatching of "prize brook trout". J. W. Hoyt set up a hatchery for whitefish at Castalia Springs, Ohio, in 1868 and F. N. Clark built one in 1870 at Northville, Michigan, for raising the same species. The Garlach and Hoyt establishments were short-livedbut Clark's hatchery was purchased by the U. S. Government in 1880 and was used until recent times for hatching and rearing a variety of species.

Ohio built four small, experimental hatcheries at Toledo, Castalia, Cleveland, and on Kelleys Island in 1875, ostensibly to test waters for a larger permanent installation, but really because of a political impasse over where to locate a single establishment. Subsequently, the main Ohio hatchery was built at Toledo and then another was constructed some years later at Sandusky. Canada opened a hatchery at Sandwich on the Detroit River in 1876 and Michigan constructed one very shortly thereafter at Detroit. Pennsylvania's Erie Hatchery began operating in 1885 with its facilities supplemented occasionally by those at Corry. The U. S. Government's Put-in-Bay Hatchery at Ohio opened in 1890. Ohio closed its Sandusky Hatchery and opened another one at Lakeside in 1903. Canada built another hatchery at Sarnia in 1908. The State of Ohio entered into competition with the U. S. Government for a number of years with the opening of a hatchery at Put-in-Bay. Ontario built two more hatcheries; one at Kingsville, Ontario, in 1917 following the closing of the Sandwich Hatchery, and another shortly thereafter at Normandale to serve the interests of Eastern Lake

Erie fishermen. New York opened a hatchery at Dunkirk in 1918, after raising Lake Erie species for some years at its older Caledonia Hatchery. The introduction and expansion of hatcheries to meet declines in important species resulted in increased resistance to other conservation measures, notably restriction on fishing.

The whitefish was the first species propagated in these hatcheries in significant numbers for planting in Lake Erie and its connecting waters. Following the chance discovery in 1876 of the use of clay to prevent walleye eggs from agglutinating[6] (Nevin, 1900), this species was raised also on an intermittent basis (e.g., at Sandwich in 1877; Detroit, 1878; Erie, 1889; etc.). Later, lake herring and occasionally carp (Cyprinus *carpio)* and yellow perch were produced. Blue pike culture was tried successfully a number of times but eggs were difficult to obtain.

The carp was introduced into Lake Erie in 1883 (small numbers may have been planted in 1882), having been introduced into the United States, to wide acclaim, after a careful and detailed study by a number of biologists (see text of Rept. U. S. Fish. Comm., Part IV, 1875-76). The introduction of carp into Canadian waters received moderate opposition (see Prince, 1925) but Canada did, on occasion, propagate them in hatcheries (e.g., at the Kingsville Hatchery as late as 1924). The U. S. Government Put-in-Bay Hatchery also hatched carp.

The fishermen generally believed that whitefish increased in abundance several years after the first large plantings (Clark, 1885). In the ensuing decades there were reports of a continued population increase and whitefish were again taken in the Western Basin where they had been scarce for some time. As a rule, fishermen and fish culturists ascribed this “increase” to the hatchery program. On the other hand, certain restrictive legislation had been partially enforced during this time, presumably permitting more spawners to reach the Detroit River.

During the early years of hatchery programs, the fish culturists actively supported a closed season during spawning, except for spawn-taking operations, and were successful in goading some agencies to institute such closed seasons. In Lake Erie, Canadian fishermen were barred from fishing whitefish and walleyes for a month during their spawning seasons in 1885 and for a number of years thereafter. The United States did not take the role of regulations as seriously as did Canada in spite of repeated resolutions by fishery experts and the efforts of fish commissions. Some restrictions were instituted, however, regulating the mesh sizes that could be used. Closed seasons were specified by the turn of the

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[6] The use of clay, swamp muck, or starch was discontinued about 1908 after development of stirring techniques that prevented agglutination.

century but could not be enforced in Ohio waters due to poorly drafted laws (Porterfield, 1902).

At about the turn of the century, “mortality factors" such as fungus (“conferva”), pollutants, and silting-over of spawning areas were *believed by some* to have affected the stocks (e.g., Knight, 1907). The concensus of almost all investigators, until about 1940, was that the major reason for the reduced catches of preferred species in Lake Erie was a too-intensive fishery (Milner, 1874a; Wakeham and Rathbun, 1897; Porterfield, 1902; Evans, 1912; Koelz, 1926; Louden, 1930). The markedly decreased catch with markedly increased fishing intensity was so common in other parts of the Great Lakes and other inland waters, many virtually devoid of pollutants, that there was no doubt as to their connection. It is only in very recent years that one occasionally finds a statement such as the one by Dymond (1964, p. 87): “. . . overfishing is seldom the cause of the serious decline of a species, especially in such large bodies of waters as the Great Lakes.” That all areas in Lake Erie were readily accessible to the fishermen in all months except January, February, and March, even before the turn of the century, was emphasized by Wakeham and Rathbun (1897). These authors, in a broad penetrating analysis, showed that catch per pound net fished per year had decreased fairly regularly in Canadian waters from 10,000 lbs. of whitefish during 1872-76 to 1,200 lbs. in 1892-94. The fact that few Canadian fishermen fished offshore in the Central Basin does not mean that these waters were largely “unfished” as is evident from comments in various sources (e.g., Wakeham and Rathbun, 1897).

That an unlimited faith in hatchery programs may have been misplaced was implied by Keyes (1894) and Post (1894). Keyes suggested that unregulated gill netting might interfere seriously with successful natural reproduction by barring the paths of, and the breaking up of, schools of migrants. Post (1894) reviewed the success of artificial propagation and concluded “that frankness compels the admission that thus far the increased catch of adult whitefish is not at all commensurate with what it seems ought to have been expected as the outcome of those great plants.”

Continued confidence in the hatchery program on the part of most fishermen (perhaps as a cover for distrust of regulations as a management approach) appears to have made the fish culturists more self-assured and less concerned about the need for protection of whitefish and other species during their spawning seasons.

The U. S. agencies swayed back toward reduced regulation and increased propagation after 1908; Canadians also reduced their regulations but maintained a moderate propagation program. Tinsley (1914) of Ontario referred in .a particularly scathing manner topersons of a view different from his own more ecological approach:

"Faddists with absurd theories presume to ignore Nature's perfect plan of reproduction, and advocate therefore emanations from their foolish delusions." But Tinsley was subjected shortly to a higher governmental authority who felt otherwise, and Canada's closed season was abolished, the amount of gear licensed increased markedly, and greater reliance was placed on propagation in Lake Erie with the construction of the Normandale and Kingsville hatcheries. Several years later more regulations were again introduced but the close restriction on the amount of gear used by Canadians was never again maintained.

To this day, no critically convincing case has been made in support of the fish culturists' stand of 1908 (see *e.g.,* Reighard, 1910) that shows that hatchery programs have been successful in maintaining or increasing yields of Great Lakes whitefish and other species over an extended period of time. Hile (1937), Dymond (1957), Christie (1963) and others have found no clear indication that whitefish or walleye hatchery programs were economically justifiable. Various bits of circumstantial evidence in the early literature (McDonald, 1909) suggest strongly that the hatchery programs did on occasion contribute to the catch. That hatcheries have *under special circumstances* been successful with salmon, trout, walleye, and some other species is now perfectly clear from both older and recent work.

Koelz (1926) made a most interesting point that the net effect of hatchery programs may have been deleterious to the fishery in permitting the fishermen to hold the opinion that so long as the hatchery program existed, overfishing for mature fish during the spawning period was impossible. This reduced emphasis on limiting the impact of fishing on the system may well have contributed to the declines of catches and the marked fluctuations since the turn of the century. We also believe that hatchery plantings could have introduced a further complication. For example, we have no idea how successful either the spawning migrations or actual spawning activities are of adults maturing from fry "dumped" into a particular part of the lake when the parents of those fry included fish that had migrated to shoals far distant from the point of release of the fry. The first walleye eggs hatched at Sandwich, Ontario, in 1877 and those hatched in 1878 at Sandwich and the Detroit hatcheries were taken from Saginaw Bay walleyes. For a number of years after that, both hatcheries obtained their walleye eggs from the spawning run down the St. Clair River from Lake Huron to Lake St. Clair and the Thames River. This area was the source of eggs, for some decades, when walleyes were being raised at Sandwich and later the Sarnia hatcheries. By about 1885, the United States hatcheries, at least at Toledo and Put-in-Bay, Ohio, and Erie, Pennsylvania, obtained their walleye eggs from the spawning run up the Maumee River. Unless all the fry died upon stocking, which we cannot accept, we can only infer that by the turn of the century the walleye population of Lake Erie was already an amalgam of originally discrete stocks from many locales.

During the past 4 decades, one hatchery after another around Lake Erie quietly has ceased operations. At some the water "went bad," at others the facilities became too old to be efficient, and sometimes the species could no longer be captured nearby or in distant waters in sufficient numbers at spawning time. In 1969, Ohio alone maintains a walleye hatching program (at Put-in-Bay).

Fishing in the period 1900-1940

By 1900, the United States fisheries of Lake Erie had passed their maximum catches of whitefish, herring, lake trout, and, of course, sturgeon. The improved steam tugs, the introduction of the gill net lifter just before the turn of the century, the increase in length and depth of gear (Ohio fished over 1,000 miles of gill nets in 1902 according to Porterfield, 1902), increased demand, the increased knowledge of fish habits . . . , led rapidly to the efficient exploitation of the sauger, blue pike, walleye, and yellow perch.

United States fisheries, faced with declining catches of the most preferred species, improved their technology and capitalized on these "second-rank" species from 1900 to 1940. Regulations were introduced and enforced, at least occasionally.

The Canadian fisheries, on the other hand, built up much more gradually until 1914, when a rapid expansion began (Koelz, 1926). These fisheries never took many lake trout, sturgeon, or sauger, and the catch of lake herring amounted to about 20 percent of the total in 1900 (the last year before herring production became markedly and irregularly cyclic). The Canadian catch built up to about equal status with the United States catch in 1920-24 and then exceeded it. Very similar trends in catches apply for lake whitefish, yellow perch, walleye, and blue pike.

Canada never reported appreciable catches of sauger, and United States landings, particularly in early years, may have been inflated by small blue pike and walleyes (Wakeham and Rathbun, 1897). A number of reports allude to the confusion about the varieties of *Stizostedion* until well into the present century. In some situations, the confusion was to the short-run advantage of fishermen, e.g., when they could sell "sublegal" walleyes as legal saugers. Reportedly this practice was occasionally followed as recently as the 1950's.

Several technological innovations stand out during the period

1900 to 1940. One modification was the setting ("canning-up") of gill nets at various depths near the surface for herring, rather than setting them on the bottom. At certain times of the year lake herring ranged through considerable depths and it then became economically worthwhile to increase the depth dimensions of gill nets 4 to 5 times thus giving rise to the so-called bull net. The latter was introduced about 1905 in the Eastern Basin and soon spread into the Central Basin. It was also efficient for taking young whitefish and lake trout. Bull nets reportedly caused the death of large numbers of the latter species and were finally outlawed in 1929 in Ohio, and in 1934 in New York and Pennsylvania.

Trap nets, which had been introduced about 1885 on the south shore and about 1890 in the Island Region, permitted more efficient fisheries because the gear was more flexible and manageable. Trap nets and fyke nets were long forbidden in Canadian waters partly because they could readily be hidden from enforcement officers and partly because they were held to be too destructive of small, immature fish.

Trap nets were fished inshore in small numbers in Ohio for several decades after their introduction. Their number then gradually increased in Ohio and later in Michigan waters; a more or less steady decline in the use of pound nets took place after 1920 and the evolution to trap nets was virtually completed by 1935. Since then, methods of fishing in United States waters have changed little.

By 1920, Lake Erie boasted 3,931 pound and trap nets in United States waters and 637 pound nets in Canadian waters. Canada and United States had each licensed about 1.4 million yds. of gill nets (United States total nets had decreased from about 5 million yds. in 1902). The pound and trap nets were fished largely in the Western and Central Basins and gill nets in the Central and Eastern Basins.

In Ontario waters of the Western Basin, trap nets began to be fished in increasing numbers about 1950, and gradually supplanted most pound nets. Several pound nets were still in operation off Pelee Island in 1969.

Fluctuations in catch, 1900-1940

The Lake Erie catches since 1900 have been characterized by marked fluctuations in species composition. Following is a general summary of observations and some reasons for the fluctuations; all of the latter remain to some extent hypothetical.

Lake trout and sturgeon catches reached peaks before 1890, and underwent a regular rapid decline thereafter. That the fate of the sturgeon was due to a too-intensive fishery is unquestioned (Harkness and Dymond, 1961). Spawning grounds for lake trout were in rocky areas of the Eastern Basin that were thought to be little affected by environmental changes in the 1920's when the population was diminishing in abundance and before its commercial extinction in 1938 (Louden, 1930). There seems little doubt now that the fishery had reduced the lake trout to very low levels; whether the sea lamprey *(Petromyzon marinus),* first recorded in Lake Erie in 1921, administered the coup de grace is unknown. If the sea lamprey destroyed the remaining lake trout they should presumably have destroyed also the burbot *(Lota* lota) as occurred years later in Lake Huron, but this did not happen. Some lake trout continued to be taken in the 1940's and 1950's, but the catches were mainly in the Western Basin where few were caught in earlier years. W. B. Scott (personal communication) suggests that these fish likely migrated to Lake Erie from Lake Huron. We consider it most probable that the remnants of the lake trout stock succumbed to the destruction of a suitable environment that resulted from the accelerated aging of the lake after World War II (Carr et al., 1965).

The runs of Lake Erie whitefish far up the St. Clair River failed long before the turn of the century (Geare, 1884) and presumably before pollution could be blamed for their decline. Few whitefish entered Lake St. Clair, the Detroit River, or Michigan waters of Lake Erie after 1920 (Baldwin and Saalfeld, 1962; Koelz, 1926).

We suspect that the gantlet of gear strung across the migratory routes of the whitefish for 150 miles must have played a major role in reducing the size of the runs. That any escaped the nets may appear a miracle. We note, however, that the pound and trap net leaders were usually of large mesh (6 to 8 in.) to reduce both water current drag and costs (Wakeham and Rathbun, 1897). Fish that did not "lead" could swim through the mesh, and natural selection over the decades might have reduced gradually the propensity of the fish to lead and thus be caught.

As mentioned previously, abundance (at least the availability) of herring, saugers, and blue pike increased markedly in the 1870's. We suggested earlier that increased fertility in the lake 1800's eventually benefited saugers, blue pike and particularly herring. Decreased predation by lake trout presumably also benefited the herring populations. Increased planktonic and clay turbidity along the Ohio shore from Cleveland westwards probably aided the light-sensitive sauger and perhaps improved also its requirements for successful reproduction (Leach, 1928; Doan, 1942).

The sauger catch attained its peak about 1916 and then gradually fell to very low levels by 1955 (Figure 3). However, the

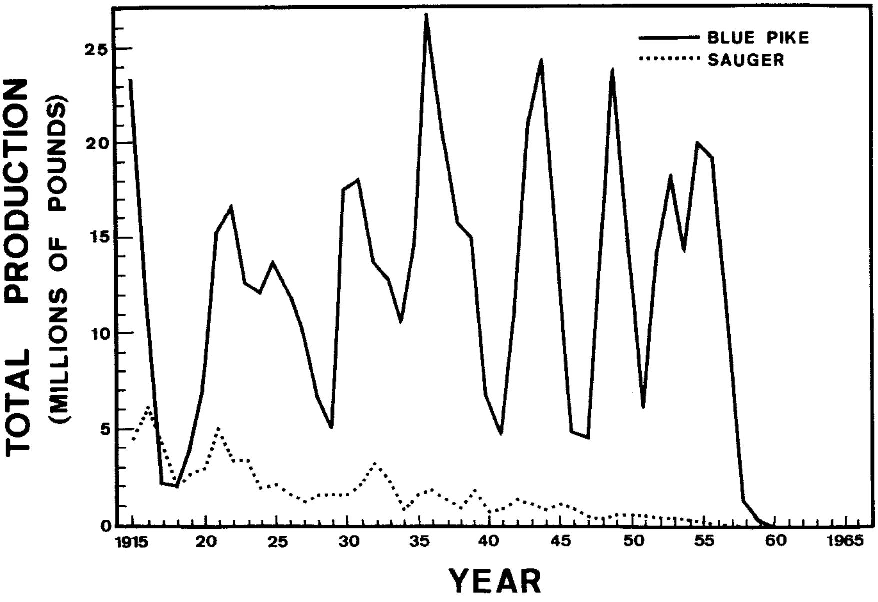

Figure 3. Commercial production of blue pike and sauger in Lake Erie, 1915-66.

confusion of varieties of *Stizostedion,* and the tendency to "lump" blue pike and small walleyes (the latter often caught in large numbers according to Wakeham and Rathbun, 1897) with sauger, should be borne in mind in examining early statistics.

The spawning runs of saugers were reported originally on rocky and sandy areas in streams and inshore waters along the south shore, particularly near Maumee Bay (Wakeham and Rathbun, 1897). The (hypothetical) spawning locations in Ohio streams along the south shore may have become unsuitable due to pollution, siltation, or damming. That stream conditions had changed is suggested by the decline in abundance of silver lampreys (Ichthyomyzon unicuspis) early in this century (Trautman, 1949).

Various pollution surveys in Ohio have shown that the shoreline has become progressively more polluted organically and covered by silt. The origin of the latter is attributed largely to ship channel dredging and, to a lesser extent, to “diatom fallout,” domestic and industrial pollution, and farm drainage. Although we believe that modifications of the physical environment ultimately had deleterious effects on the sauger, we believe that the ever-increasing amounts of gear fished (until very recent years) also must have taken their toll on the capacity of the population to maintain its abundance. Since the decline was fairly regular, we suspect, however, that environmental conditions were very important limiting factors.

The clay turbidity along the south shore may have reached its maximum early in this century and then gradually decreased, due presumably to progress in erosion control (Van Oosten, 1948). Recent data suggest another upswing in turbidity that is traceable to increased ship channel dredging in western Lake Erie. The earlier decrease may have brought turbidity into a range more favorable to the sauger's relative-the walleye. The abundance of walleyes gradually increased as saugers declined. In direct competition with saugers, walleyes should have an advantage in somewhat clearer water, judging from their relative abundance in various parts of the same body of water where both occur.

The competitive interactions between blue pike and either saugers or walleyes were probably not major. The blue pike's habitat was farther offshore than that of the sauger and walleye. Larger walleyes probably moved into deeper waters in appreciable numbers in summer (Wakeham and Rathbun, 1897; and others) but here they would most likely feed on larger fish than did the blue pike and thus not compete directly with them.

After its early increase in abundance about 100 years ago, the blue pike remained abundant for 3 or 4 decades. At the end of this period, about 1910, its numbers began to fluctuate violently (Figure 3). We suggest that the fluctuations were due to an over-intensive fishery which ultimately applied too much stress to those self-stabilizing mechanisms that this population and its ecosystem had evolved.

The blue pike is a predator on small organisms. Presumably its young-of-the-year frequented deep, sandy, and rocky shoal areas where they were vulnerable to some extent to predation by older members of the population. When production is sufficiently high, including large incidental catches of many small blue pike, the aforementioned self-regulatory mechanism would fail in that too many young-of-the-year would escape predation. There would then be a brief population explosion followed by several years of small year classes due to too-intensive predation by the old upon the young. As the population of old fish decreased, another upsurge might result. In a non-exploited, reasonably complex ecosystem, these oscillations likely would soon damp themselves out (except perhaps with very short-lived species). Conversely, good markets and a flexible, unregulated, intensive fishery would, if anything, lead to an increase in the amplitude of the oscillations since the fish also would be caught even when they were scarce. The end of this succession of increasingly violent fluctuations might be the economic or even biological extinction of the species at some low point of abundance. Ecologists have occasionally reported the occurrence of similar sequences (Odum, 1959).

The regular spacing of the peaks of blue pike production

(Parsons, 1966), at periods of about twice the length of time it required for a year class of blue pike to achieve peak reproductive capacity and also be decimated by the fishery, is what we would expect in an oscillating system in which the major predator is cannibalistic and is itself oscillating in abundance. We believe, therefore, that cannibalism on fry and fingerlings was the major mechanism responsible for these fluctuations from 1910 to 1950, but recognize that other more indirect mechanisms might have played the main role since 1950.

We consider it likely that a too-intensive fishery was largely responsible for the "crash” decline of the lake herring after 1924. This “crash” coincided with the rapid increase in gill nets licensed in Canadian waters at a time when the American fishery was already very intense and still increasing in fishing effort. The notorious bull nets were used commonly in this period until outlawed in Ohio in 1929 and in New York and Pennsylvania in 1934.

Inearlier years, the majority of herring and whitefish apparently migrated regularly to the extreme eastern margin of the Central Basin and at least some moved into the Eastern Basin in early summer; a reverse migration occurred in early autumn (Wakeham and Rathbun, 1897). Ontario fishermen of western Lake Erie caught, practically speaking, no herring after 1920; fishermen of the Central Basin caught practically none after 1925 except from 1945 to 1947 (Davies, 1960). The Eastern Basin had two short peaks of abundance after 1928. This west-to-east temporal progression in the almost complete initial failure of the fishery (1920, 1925, 1929) coincides with the relative probability of capture of a migrating fish for the decades following 1920 - very high for herring moving to the west edge of the Western Basin, high for those moving to the west edge of the Central Basin, and moderately high for those remaining in the Eastern Basin. We propose this progression as evidence that the fishery collapsed due to an intensive fishery.

Wakeham and Rathbun (1897, p. 78) referred to an earlier collapse of the herring thus:

“In looking for the cause of the decrease in the western catch, we find that during several years prior to 1890 this species was being taken by the pound nets in certain places in somewhat reduced numbers. Then came an abrupt and very pronounced falling off, which was first manifested at Port Clinton in 1890, at Huron and Vermilion in 1891, and about the Bass Islands and Kelleys Island in 1892. This sudden drop occurred immediately after the extension to the Western Basin of the heavy gill net fishery which had previously been confined to the deeper waters. The tugs belonging at eastern ports had started the practice of following up the schools of herring during their fall or spawning movement, and, deriving great profit in that connection, they were joined by the local tugs in operating in the Western Basin and adjacent to its eastern border."

They made a further very interesting point: "The statistics do not favor the view that the decrease has been produced simply or solely by the taking out of too many fish. The prevailing opinion among the fishermen is to the effect that the course of the schools had been diverted by the many nets, which prevent their reaching the Western Basin except in relatively small numbers, and causes them to occupy other than their customary grounds in late fall. It is said that large bodies of herring have been spawning in recent years off the south shore between Huron and Fairport, where such an occurrence was previously unknown, but the statements in that regard lack confirmation. A very reasonable deductionis that, being prevented from reaching their proper spawning grounds, their eggs are largely deposited in situations not suitable for that purpose, with the result that the productiveness of the species has been impaired."

We might add that if individuals of a homing species return to an imprinted spawning locale, even a marginal one, then any progeny would home to that marginal spawning area, even if better grounds became accessible again in subsequent years, unless, of course, a strong instinct overpowers the imprint. We know very little about the relative roles of instinct and imprinting in migrating fish.

Following the "crash" of 1924, the herring staged two brief recoveries in abundance. That a small residual stock managed to escape capture to spawn successfully (when fishermen were no longer seeking them out), and that the condition of the ecosystem was such that a relatively strong year class was produced in 1943 (Scott, 1951) do not contradict our suggestion of fishing as the principal destructive factor. The herring can stand moderate crowding in its ecosystem where it feeds on planktonic animals. The species produces a large number of eggs that are broadcast in areas chosen in some manner by the fish. Its young are probably not vulnerable to cannibalistic attacks. Given these conditions, an ecologist would expect that small numbers of spawners would normally give rise to small numbers of young, and would expect a large year class to arise from a small spawning stock only when environmental conditions were exceptionally favorable (Beverton and Holt, 1957, Section 6; Ricker, 1958, Chap. 11). In taking this position, we disagree explicitly with the views of Dymond (1964) **that overfishing is seldom the cause of the serious decline of a** species, especially in such large bodies of water as the Great Lakes and that there are usually enough adult fish left by the fishery to produce an abundant crop if conditions are favorable. One can infer certain special circumstances of population biology and fishery practices where an intensive fishery would not reduce the probability of reproductive success, but any such special circumstances that occur to us could not have applied to Lake Erie's herring from what we know of the pre-1940 history of this species.

There is, at this juncture, a very important general point to be made concerning fishing intensity. It often seems to be assumed that once a species falls to low levels of abundance it is no longer taken because it is unprofitable to do so. This is not true, however, when certain circumstances apply as in the Lake Erie fishery, to wit:

1. If the species either schools or migrates to well-defined spawning areas, it may well be profitable to take most of the "last ten thousand" fish of a population;
2. If the species at some period of the year occurs in waters where other species are fished intensively, and is vulnerable to the gear, it can be reduced further in numbers even if already at a very low level of abundance;
3. If two species of low abundance can be caught together, thus making it profitable to fish both where it would not be economical to fish either alone; or,
4. If fishermen have a work obsession or a compulsive reluctance to give up a life-time trade that forces them out onto the lake even when it is uneconomical for them to go.

An examination of the history of the relative abundance of species and of the fishing practices and intensity in Lake Erie shows that one or more of these conditions can be demonstrated to have existed almost every time a valued species dropped to a low level. In fact, the above-listed "Condition 3" applied in 1966 as the Canadians harvested small walleyes and white bass together in "canned" 3-1/2 in. mesh gill nets.

Before we proceed to more recent history, we should refer to the great turbidity vs overfishing duel begun in the 1930's (Langlois, 1946; Van Oosten, 1948). Langlois held that clay turbidity, due largely to poor farming practices in Ohio and Indiana, was responsible chiefly for the decrease in Ohio catches. Van Oosten argued that a largely unregulated, exploitive fishery was to blame.

On the basis of a re-examination of the data and some tentative conclusions already elaborated, it is our opinion that both were, in part, correct. We believe that turbidity from poor erosion control on Ohio farmlands played a role in reducing the catch of whitefish and lake herring along the southwest shore. Furthermore, we believe also that Ohio's trap net fisheries of the 1930's were not as excessively exploitive as most gill net fisheries of that period. In many other parts of the Great Lakes, however, turbidity played no role in the decrease of catches and, as pointed out by Van Oosten, unregulated fishing practices were clearly to blame.

Fluctuations in the catch, 1940-1966

The changes in fish populations of previous decades cannot compare with the dramatic fluctuations since 1940 which culminated in the commercial extinction of the fisheries for whitefish, herring, and blue pike.

We do not know whether blue pike or other fish (e.g., perch) preyed on young herring, though we suspect that they did. If so, this fluctuating, predatory pressure would have contributed to instability in the lake herring stock. A number of confounding factors prevailed which discourages any temptation to test this possibility with existing data. Whitefish and herring thrive in waters showing some mesotrophic characteristics (R. A. Ryder, unpublished data). Perhaps even the Eastern Basin has become too eutrophic for these species, since in recent years the oxygen saturation of the hypolimnion was less than 50 percent in summer (Carr, 1962). How much stress this would place on these fishes is not known. We suspect that in addition to a continuation of patently exploitive fishing practices, some critical threshold in accelerated eutrophication was passed between 1940 and 1945 (Carr et al., 1965) which altered the environment to the extent that it affected the abundance of many important species.

It is clear from our knowledge of recent oxygen and temperature conditions that the Central Basin could no longer support whitefish and herring in summer during the past decade except, perhaps, in a fringe near the eastern edges. We do not know when conditions in the various parts of the basin became critical, but some degree of oxygen deficiency occurred occasionally in the southwestern parts of the Central Basin as early as 1928 (Carr, 1962). Most, if not all, of. the whitefish migrated out of this area each summer even before the turn of the century (Geare, 1884); herring behaved similarly (Wakeham and Rathbun, 1897). Some groups of whitefish and herring remained all summer in the Central Basin, however, even as late as the 1940's (W. B. Scott, personal communication).

For any cold-water species spawning in the Western Basin, too rapid de-oxygenation of the Central Basin hypolimnetic waters would presumably trap the young when they migrated back to the east. The Western Basin is (theoretically) flushed-out in about 2 months, almost entirely by Detroit River water. Thus, passive transport might carry young whitefish or herring hatched in the Detroit River or Western Basin proper in early April into the Central Basin by early June. Recent observations (see e.g., Carr, 1962) indicate that these young, assuming they require cold water, would have to proceed about 50 miles northeastward in 2 months to find favorable conditions. We do not know the rate at which such small fish would migrate nor whether the migration would be suitably directed.

Lawler (1965) suggested that the slight warming trend recorded for the climate of the Lake Erie region may have permitted water temperatures in winter to remain sufficiently far above the ideal incubation temperatures for lake whitefish (0.5° C.; 0.9° F.) to impair hatching success. Furthermore, at slightly raised winter temperatures, hatching would occur before suitable food became available with the spring plankton blooms. Water temperatures at or near the surface of the substrate could have been held above 0.5° C. (0.9° F.) by increased decomposition of organic materials carried into the waters, or synthesized there. ZoBell, Sisler, and Oppenheimer (1953) have demonstrated that the temperature of bottom muds can be considerably higher than that of the overlying water.

Whether the foregoing factors were critical on the spawning areas of the Western Basin is not known; even if they were not, we suggest that oxygen deficiencies in the Central Basin eventually became critical for the whitefish. We believe that oxygen deficiencies in the hypolimnion of the Central Basin were also involved directly in the population fluctuations of smelt, and perhaps blue pike, but less directly for those of the walleye and yellow perch.

Blue pike reportedly frequented deeper waters, at least deeper than 40 ft., as summer progressed. In the Central Basin of Lake Erie the characteristically very “steep” metalimnion occurs normally at depths of 50 to 60 feet. ‘Whether the blue pike actually preferred to remain in this cooler water of less than 60° F., with an epilimnion of about 75° F., is not known. In past decades fishermen caught blue pike in summer from deeper waters off Vermilion, Ohio, that came to the surface “hard and frisky.” This implied to the fishermen that they came from cold bottom waters (M. Hosko, personal communication).

Limited “test netting” in the 1950’s indicated that the blue pike inhabited the lower epilimnion in the eastern part of the Central Basin (Ontario data). Since blue pike were caught in numbers in the epilimnion along the northern margin of the Central Basin even in late summer (Kennedy, 1961), we suggest that although they preferred to remain in cooler waters, some did not remain there consistently. The eastward movement of blue pike to somewhat deeper waters off Fairport, Ohio, is consistent with the observation that oxygen concentrations in the hypolimnetic waters of the Central Basin first fell to low levels off Vermilion in summer, then spread north and east.

The larger individuals in some populations of walleyes migrate in summer to colder, deeper waters. Recent tagging studies show that most western Lake Erie walleyes remain in that basin through the summer (Wolfert, 1963); whether or not some of these fish and those from the Central Basin frequented the hypolimnion of the Central Basin in earlier years is not known. By 1959, oxygen concentrations in the hypolimnetic waters off Fairport, Ohio, (the area fishermen of earlier years called "blue pike heaven") were less than 1 ppm. Low oxygen has recurred in subsequent years, and we do not know in how many previous years it also may have been low. From what we know of the preferred habitat of the *Stizostedion* species, we suspect that they tolerate low oxygen concentrations, perhaps down to 5 ppm, somewhat better than do whitefish and herring but less well than still-water species, like the bullheads and carp. We suspect, however, that at oxygen concentrations below 5 ppm the stress on a *Stizostedion* becomes sufficient to cause it to move to waters of higher oxygen concentration.

The *Stizostedion* species, other percids, and many other species rest on the bottom for part of each day, night, or both. What effect an enforced pelagic existence has on such species is not known. Data collected during fishery surveys show that *Stizostedion* species, other than fry, are seldom taken far offshore where waters are either deep (greater than 80 feet) or overlie an oxygen-poor hypolimnion. If this is true, then a growing area of oxygen-deficient waters off Vermilion would provide a sanctuary of increasing size in the epilimnion or metalimnion for pelagic species preyed on by the perch and *Stizostedion* species. The metalimnion of the Central Basin often has such a sharp temperature gradient (about 5° C. per m.; 9° F. per 3.3 ft.), that few species are likely to be comfortable there. It appears from surveys made by Ontario in 1962-63 that young-of-the-year and yearling smelt and perch are the most common fishes at the bottom of the epilimnion in the Central Basin (unpublished data). Older perch apparently have a regular offshore-onshore movement (Scott, 1955), and older smelt move eastward as the summer progresses (Thomasson, MS, 1963).

The interrelationships we now postulate, although admittedly speculative, indicate the complexity of the situation. The greater the area of hypolimnion with insufficient oxygen, the greater the restriction on walleye mobility, and, therefore, the greater the survival of the pelagic young of smelt, perch, and other species on which it feeds. Blue pike, though crowded more (low oxygen might limit their spawning to the eastern edge of the Central Basin), should have a surplus of food and grow rapidly. The oxygen stress on blue pike would increase their movements and thus make them more vulnerable to fishing gear (F. E. J. Fry, personal communication). Catch rates might well increase and the (proposed) cannibalistic habit of blue pike diminish. Any decrease of cannibalism should "damp out" the oscillations of year class strength. Catch records for blue pike are consistent with such a process becoming effective about 1950.

An expanding Central Basin sanctuary for pelagic, eurythermic young fish should permit more of the young to survive and their populations to increase, Besides smelt and perch, the young of sheepshead[7] *(Aplodinotus grunniens)* and white bass also frequent the shallower waters of the Central Basin. All showed marked increases in abundance beginning about a decade ago.

Adult smelt first appeared in very large numbers at the western end of the Central Basin in 1951 (Kennedy, 1961). These fish were probably the 1948 year class, which suggests that a large sanctuary existed by 1948. Smelt were not harvested in significant numbers until 1952, and not intensively until 1960. Very large numbers were present in 1953 and 1954, judging from the numbers caught accidentally in the fishermen's large mesh nets. They continued to be abundant in spawning runs at Pt. Pelee until 1962, then declined somewhat.

The year classes of blue pike and walleyes were weak after 1954. Blue pike never again spawned successfully, and walleye populations which spawned on grounds immediately adjacent to the Central Basin and, apparently, some in the Eastern Basin suffered a similar fate. With the exception of a subpopulation of walleyes near the New York shore of the Eastern Basin, none have recovered since.

That a dominant yellow perch population can restrict walleye populations to a low level of abundance has been suggested by a number of workers (Carlander, 1950b; Moyle, 1949). The European perch and sander have interrelationships similar to the yellow perch and walleye (Tesch, 1965). If the yellow perch become very abundant, and are cannibalistic, and are harvested with reasonable intensity so that relatively few survive beyond 3 full years, we would expect a 3-year cycle of dominant year classes if spawning conditions remain consistently favorable. Recently, perch have produced strong year classes every three years in western Lake Erie. If perch were very abundant, we would expect that perch and walleye fry would be decimated by the perch. This predation would tend to put the cycle of larger year classes of walleye in phase with those of the perch which is precisely what has happened in recent years in western Lake Erie (unpublished U. S. Bureau of Commercial Fisheries data).

The expected cycle for smelt is somewhat different. Adult smelt migrate eastward across the Central Basin after spawning

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[7] The approved common name of this species "freshwater drum" has no currency anywhere in the Lake Erie basin where the fish is almost universally called "sheepshead."

at Pt. Pelee. Yearlings and young-of-the-year are found near the thermocline throughout the summer. Yearlings, therefore, should feed on young-of-the-year, causing an alternate year cycle of abundance (spawning conditions being consistently favorable). This alternate year cycle has existed during the past decade. The cycles of the Eastern Basin might be quite different, depending on the spatial distribution of year classes of smelt about which we know relatively little. It is clear from preliminary studies of Ontario data that yearlings and young-of-the-year are not compressed into a thin horizontal layer in the Eastern Basin as in the Central Basin.

Smelt and perch have maintained relatively high levels of abundance for about 15 years. As outlined above, both species seem to have relatively good self-regulating mechanisms that prevent populations from becoming excessively crowded. Both species feed on invertebrates (plankton or benthos, or both) as well as fish and thus are not likely to starve, even at high population densities. Both species spawn at a young age - 2-3 years.

Market demand for smelt and perch is at best moderate. It has not been worthwhile to fish for them very intensively. The economics of the American industry have made it, in fact, largely unprofitable to fish commercially for them on the south shore (the Lake Erie fishery is now in a sense reversed from what it was at the turn of the century when it was "uneconomic" for Canadian fishermen to take large catches, since they could not sell them). Thus, there is no serious danger that smelt or perch will be taken long before they mature sexually, or that they will be barred by nets from their spawning grounds.

Still important, however, is the fate of those few walleyes that persist in the Western Basin and stray into Canadian waters. Some spawning grounds in the Western and Eastern Basins still yield walleye fry. There seems no reason why the walleye population would not increase in abundance if protected and perhaps challenge the yellow perch for dominance in the Western Basin (see following sections). With a steady, moderately intensive fishery for smelt, the various walleye populations around the periphery of the Central Basin might expand again and form the basis for reasonably profitable fishery.

In this brief history of fish and fishing in Lake Erie we have drawn attention to what we believe were the main processes in the lake ecosystem during the past century and a half, especially for the walleye; what were, from time to time, considered to be the solutions to recurring problems; and the relative success of various proposed solutions. We consider that this order of complexity is minimal if one examines the real essence of such problems as how to manage the walleye in Lake Erie. The simple model, the simple analysis, and the simple solution can be counted on merely to aggravate practical problems in a fishery.

THE WALLEYE IN WESTERN LAKE ERIE

Our purpose in this section is to consider the general information, concepts, and findings of the preceding sections in relation to the present habitat and niche of the walleye in western Lake Erie. For the words "habitat" and “niche” we use the connotations given by contemporary ecologists, e.g., by Odum (1959, p. 27). The habitat is the place where the organism lives. The niche is the position or status of the organism within its ecosystem resulting from the organism’s structural adaptations, physiological responses, and specific behavior (inherited, learned, or both). In our consideration of the walleye’s niche, we leave out for the moment its interactions with man as a predator and consider these separately in the next section.

For management we need to know particularly if the ecosystem can support larger populations of walleyes. In which aspects, if any, do biotic and abiotic components in various geographical parts of Lake Erie not provide the essential requirements for the species? Stated otherwise, and without intending to imply an over-simplified approach-what are the limiting factors?

In our analyses, we examine the adequacy of spawning grounds, effects of hatchery programs, types of natural mortality factors, availability of suitable habitat for various life stages, food organisms, competitors, predators, and the possibility of introgression. Finally, we address the problem of the size a population of walleyes might attain in western Lake Erie under sounder management than has been applied recently.

Spawning grounds

We have already referred in an earlier section to walleye spawning, spawning runs, and related biological phenomena in a number of different contexts. We assume that a walleye fry imprints some essential characteristics of its birthplace and that most sexually mature adults return to that birthplace to spawn. Under such conditions, a variety of somewhat different forms can persist for centuries, sympatric for most of their lives, but segregated at spawning times.

Wakeham and Rathbun (1897) referred to walleye spawning grounds in Lake Erie as occurring “in the bays and streams as well as upon the reefs and along the greater portion of the shore but principally in the western end of the lake. The vicinity of Maumee Bay appears to be the most prolific spawning ground in Lake Erie, and the Thames River holds similar rank in the Lake St. Clair region." We doubt that walleye spawning sites were that abundant. Walleyes were still a "second rank" species (in market preference) and the fishermen were not actively seeking spawning aggregations as they were of the whitefish, herring, and lake trout. We suggest that, for these reasons, fishermen did not know in as much detail where all the walleyes spawned as they did for the aforementioned "first rank" species.

For a number of years after 1880, personnel of the Sandwich Hatchery collected eggs from ripe walleyes at Bois Blanc Island and other locations in the Detroit River. We infer, therefore, that spawning runs once occurred there, but that they were either small or did not persist long. This hatchery subsequently obtained its eggs from a Lake Huron run into the St. Clair River for at least two decades starting in 1886 (see relevant Ann. Repts., Dept. of Fisheries, Canadafor years 1886 through 1908). The Detroit hatchery also obtained its walleye eggs, in some years, from the Canadian side of the St. Clair River which suggests that walleye runs to the lake shores near Detroit were small. Goode (1884) also indicated that spawning runs to the shores near Detroit were small.

Langlois (1945) stated that early records showed that 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." According to Langlois, most of these runs had been destroyed by 1945 due to construction of dams, siltation, excessive pollution, or irregularity of stream flow due to man's activities.

Some adult walleyes tagged during the 1967 spawning season in Sandusky Bay were captured within a few months as far away as Lake St. Clair (J. V. Manz, unpublished data). These recoveries may indicate a spawning run of Lake St. Clair walleyes into Sandusky Bay. Trap net fishermen near the edge of the Western Basin suspect this migration since many large or "jumbo" walleyes can, on occasion, be caught here during the spawning season when very few large fish were taken in the Western Basin in the preceding autumn (e.g., M. Hosko, personal communication).

Young-of-the-year walleyes are sometimes found in moderate **numbers in the Western Basin in autumn even though very few** were caught there earlier in the summer (J. V. Manz, unpublished data). This enigma can be resolved if one postulates a late-summer movement of some young-of-the-year walleyes from Lake St. Clair into western Lake Erie. There is some evidence of such movement in U. S. Bureau of Commercial Fisheries trawl catches.

Juvenile walleyes were tagged during the 1967 spawning season on the south shore of Lake St. Clair near Belle River. Some of these fish were recaptured within several months in western Lake Erie (R. M. Christie, unpublished data). The recoveries support the inference of a spawning run from western Lake Erie to Lake St. Clair. Tagged adults in the runs up the Thames River of Lake St. Clair have migrated back to Lake St. Clair and Lake Huron.

Canadian fishermen recall runs of ripe walleyes to sand and gravel areas on the west shore of Pt. Pelee and also along the north shore of Lake Erie near Kingsville (W. H. Krause, personal communication). These areas have been used by few, if any, walleyes in recent years. The grounds off Pt. Pelee have become progressively modified over the past 20 years by a black, malodorous deposit noticeable on trap net anchors. The changes are probably due to domestic and cannery pollution from Leamington and other communities. According to fishermen, various reefs off Pt. Pelee and inshore areas off Pelee Island had large spawning runs until relatively recent years (H. Tiessen, personal communication). These runs are now either small or extinct.

Spawning runs of walleyes persist in two Ohio streams, the Sandusky and Maumee Rivers. The size of the latter run may be increasing (J. V. Manz, unpublished data), perhaps as a result of some recent progress in pollution abatement and because few Ohio commercial fisheries in this area have survived recent biological, economic, and political events. In a search for young-of-the-year walleyes in the early summer of 1967, a large concentration was found in the mouth of the Raisin River in Michigan. The presence of several dams and the grossly polluted conditions now prevailing in the lower Raisin River and its estuary seem to eliminate the possibility of a spawning run in this river. We can only conclude that these young walleyes originally came down the Detroit River or from one of the Western Basin's offshore reefs.

Today, the major existing spawning grounds, shown in Figure 4, are the Kelleys Island-Bass Island reef and shore areas and, the reef area southwest of the Bass Islands close to the shore of Lake Erie (Baker and Manz, 1967). These reef areas are, from all indications, free of mud, silt, and clay. The currents are strong enough to move large sand particles, thus tending to keep the offshore rocky reefs scrubbed clean (Hartley, 1961; Hartley, MS[8] ; Hartley, Herdendorf, and Keller, 1966). Circumstantial

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* Hartley, R. P. Preliminary report on the 1962 survey of bottom sediments in the southeastern part of the Central Basin of Lake Erie. Prepared in 1963 for Ohio Dept. Nat. Res., Div. of Shore Erosion. Unpublished manuscript.

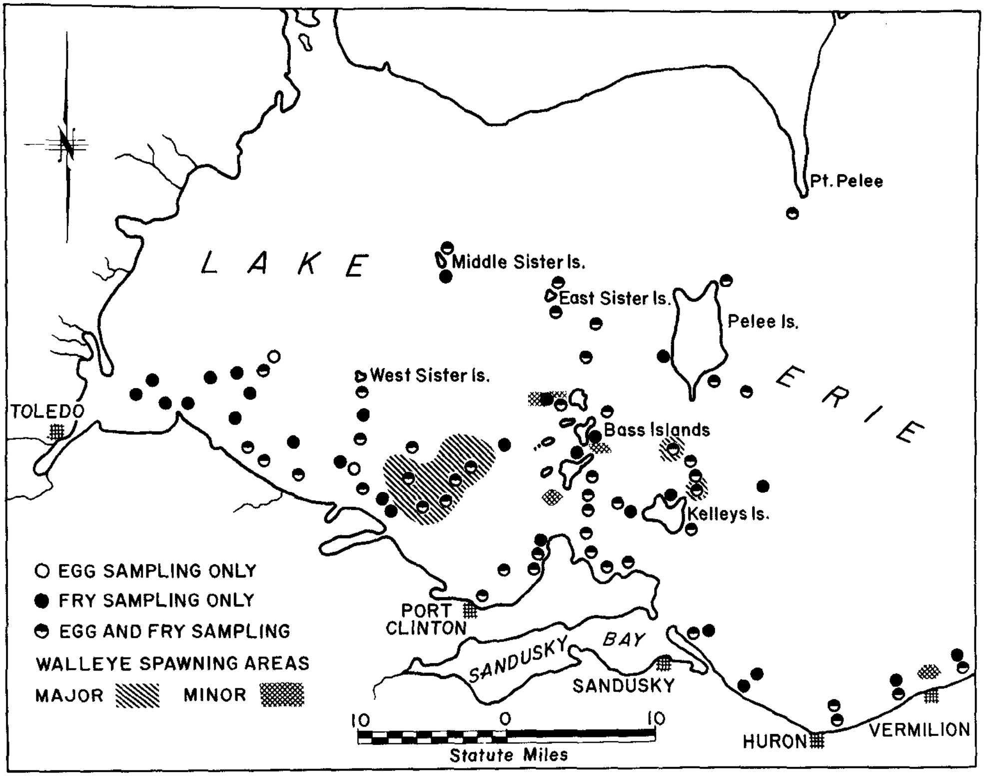

Figure 4. Walleye spawning areas in the Western Basin of Lake Erie and stations where eggs and fry were collected by the Ohio Division of Wildlife.

evidence suggests that attached "moss" may have increased in abundance on the Kelleys Island reef in recent years (J. V. Manz, unpublished data). Some Canadian fishermen also mention similar algal growth on some Canadian reefs in the Central Basin. The increased fertility of waters in the southwest corner of the Central Basin may be responsible for these algal growths.

That the Ohio reefs of the Western Basin have been used by the walleye, year after year, until the present was documented by Baker and Manz (1967). Other references to their findings are given in a preceding section on walleye ecology. Neither smelt nor commercial fishermen are found commonly over the Ohio reefs during the spawning period; the fishermen are prosecuted, if apprehended. Fishermen in small boats, however, do set gill nets (legally) near to, but just off, the reef areas to intercept spawners.

It is clear that the deeper waters and eastern edges of the Western Basin have become modified to the extent that ripe walleyes are no longer taken there in significant numbers. This suggests that spawning grounds in these areas have been ineffective in recent years and that any runs that may have homed to these sites have now disappeared. We believe that the aforementioned runs to areas immediately adjacent to the Central Basin may have failed due to excessive predation by yearling smelt upon pelagic walleye fry. The failure of the walleye populations to recover in strength in other inshore areas around the Central Basin after their collapse in the late 1950's, even though some of these areas are not heavily fished, is consistent with this hypothesis. A small population persists in the New York waters (under protective legislation) in an area where small smelt may not be abundant during walleye spawning periods. The spawning runs of smelt into the streams of New York, Pennsylvania, and Ohio are small (H. A. Regier, unpublished data).

Direct and circumstantial evidence indicate the persistence in 1967 of spawning runs of walleyes from western Lake Erie into a number of streams, to certain reefs, and to adjoining Lake St. Clair and its tributaries. Other large runs of earlier years are now small or extinct. Some "straws in the wind" suggest that several walleye runs may be increasing slowly in recent years. We believe increased efforts in pollution abatement and increased survival of older walleyes due to reduced fishing intensity would make it possible for these runs to improve their reproductive potential. The evidence does not indicate that the limited area of suitable spawning grounds are saturated by spawners. Furthermore, any increase in the number of these spawning areas that might result from reduced pollution should act to increase population size by insuring greater year-to-year consistency in reproductive success.

If spawning runs are to areas that differ limnologically *(e.g.,* stream beds, lake shores, island shores, reefs), or are separated by moderately large distances (some tens of miles), then it is unlikely that so many accidents would occur in a particular year that all, or almost all, walleyes would experience reproductive failure. Conversely, if the number of runs decreased progressively, we expect "year class strength" to show a downward trend and a greater variability from year to year. The evidence indicates clearly that both of the latter circumstances have occurred in western Lake Erie and we believe they are causally related. We believe that some of the runs were destroyed by pollution, and that some of the remaining spawning grounds currently in use have been impaired by pollution. This view is not intended to suggest that the intensive fishery was blameless. As already indicated, we believe that the fishery was partly responsible for the explosion of smelt and that these, when dominant, probably consumed vast numbers of walleye fry from spawning grounds surrounding the Central and Eastern Basins.

Hatchery programs

We have not attempted to relate numbers of walleyes stocked in Lake Erie in various years with subsequent year class strength and have no direct measure of the effects of the current walleye hatching program of Ohio's Put-in-Bay Hatchery. Ohio has, from time to time, established excellent self-sustaining walleye populations in moderately eutrophic, inland waters by planting fry. Information on the rates of success in these experiments has not been published.

Scott, Omand, and Lawler (1951) experimented with raising walleye fry in a small reservoir adjacent to Lake Erie's Eastern Basin and released fingerlings into the lake. The stock apparently contributed to the fishery, but not in economically satisfying amounts.

Minnesota, Wisconsin, Iowa, New York, and several more southerly states maintain hatchery programs for stocking walleyes in new, rehabilitated, or ecologically marginal waters. Minnesota has experimented for decades with walleye culture and stocking programs and uses fry and fingerlings under somewhat different circumstances (Anon. 1964).

J. L. Forney (personal communication) has found evidence that during May a high proportion of the pelagic fry in Oneida Lake are of hatchery origin. In Clear Lake, Iowa, the results of alternate year fry stocking indicated hatchery fry contributed appreciably to the walleye fishery (Carlander, Whitney, Speaker, and Madden, 1960). In both lakes over 3,000 fry were stocked per acre.

It is questionable whether a walleye hatching program contributes anything to the stock when walleyes are abundant (Hile, 1937). Under the present circumstances in Lake Erie, however, a well-managed hatchery program may make an important contribution. In the absence of a more thorough analysis, we can neither endorse nor condemn the Put-in-Bay Hatchery operations.

Habitat and natural mortality of young walleyes

Forney (1964) found that walleye fry are normally pelagic for about 4 weeks after hatching. Because sac fry remain initially near bottom, dispersal of stocked fry in Oneida Lake can be predicted from measurements of bottom currents for a period of 2 to 3 days (Houde, 1967). After absorption of the yolk sac, fry concentrate from 1 to 12 feet below the surface. Wind-induced surface currents apparently transport the fry and concentrate them in semi-protected bays. Dispersal of fry from spawning areas in Oneida Lake may be limited to the first 5 to 8 days following hatching since few older fry are taken in open water (J. L. Forney, personal communication).

In spite of extensive attempts to find them, walleye fry have not been taken in sufficiently large numbers in western Lake Erie to indicate their movements. If they are distributed by wind-driven surface currents or the more regular currents of the water mass, certain ecological implications follow. Prevailing westerly winds or storms, often from the southwest, would tend to sweep pelagic fry from reef or shore areas along the western edge of the Central Basin into the Central Basin proper. At least in some years, yearling smelt are abundant in these waters at this season and we suspect they would prey on the walleye fry.

Similarly, the regular southeasterly current through the Pelee Passage, between Pt. Pelee and Pelee Island, would carry some fry from adjacent reef areas into the Central Basin. Furthermore, the predominant flow of the currents in the Island Region and the Ohio reefs is eastward (Carr and Applegate, MS[9]). When westerly winds are strong, these currents would sweep the walleye fry into the Central Basin before they became benthic. Smelt tie not common west of Pelee and Kelleys Islands except in winter, but are abundant in the water strata of the Central Basin into which the fry may be carried (J. V. Manz, unpublished data).

Judging from direct observations, fishermen's catches, and tagging studies, most walleyes, including fingerlings, are relatively sedentary in summer. Fingerling walleyes were distributed predominantly inshore during June and early July on or near shallow, sandy, or weedy areas in Oneida Lake (Forney, 1966). They have been found in similar places in Lake Erie (J. V. Manz, unpublished data). In Oneida Lake they move gradually offshore in summer and by October most young are at depths of 20 to 40 ft.

Protected areas in southwestern sections of western Lake Erie, some decades ago, had extensive beds of rooted, aquatic plants

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[9] Carr, J. F. and V. C. Applegate. The surface currents of Lake Erie. U. S. Bur. of Comm. Fish., Ann Arbor, Mich. Unpublished manuscript.

(Langlois, 1946). These had disappeared over 25 years ago, due presumably to:. increased clay turbidity from shore erosion; ship channel dredging; farm runoff; destruction by carp; and, increased plankton blooms from enrichment by agricultural fertilizers and industrial and domestic sewage from Michigan, Ohio, and Ontario communities. In spite of these changes, western Lake Erie presumably contributed large numbers of young to the high walleye production of the 1950's. Therefore, rooted, aquatic plants cannot be in themselves a critical component in the environment of fingerling walleyes. Almost the entire south shoreline is covered with sand overlying hard clay (Verber, 1957). We have no evidence that these shoreline areas have changed substantially since 1945 (cf. Anon., 1945, and Verber, 1957). We have, therefore, neither direct nor circumstantial evidence from which to argue that the habitat for fingerling walleyes has deteriorated in any way in recent times.

Autumn is a time of movement for walleyes, judging once again from the fishing success of stationary gear and from tagging studies. Young-of-the-year in Lake Erie have also been shown to undergo extensive migrations during autumn and winter. Some young-of-the-year tagged in September of 1959 off Pt. Pelee were caught the next spring on the south shore of Lake St. Clair. Presumably young-of-the-year walleyes are as active under the ice in winter as are the adults. Aside from possible predation (discussed later in this section), we know of no abnormal environmental conditions that might occur in western Lake Erie that would cause an unusually high mortality at this stage of their life.

Habitat and natural mortality of older walleyes

We are satisfied, but with some reservation, that the condition of the habitat in Lake Erie for older fish is reasonably good. In the section on general ecology we discussed the effect of light intensity on walleye vision, and the preference for hard clean bottom-a preference that we attributed to a respiratory apparatus poorly adapted to oxygen concentrations much below saturation levels. We know that these two requirements are now submarginal in some periods of some years in parts of the Western Basin (Carr et al., 1965). Other limnological conditions of the Western Basin (summer temperatures, total dissolved solids, alkalinity) appear to be well within the range tolerated by the walleye. We should not overlook entirely the possibility, however, that modern industries may have accidentally produced wastes that are highly toxic to the walleye but less toxic to other cohabitants of the area (Applegate and King, 1962).

We judged from R. A. Ryder's classification mentioned earlier, that walleyes prefer water of a transparency between 4 and 10 ft. (Secchi disc). Transparency isoclines for western Lake Erie estimated from data collected in 1961-1963 are shown in Figure 5. The summer and autumn data have been plotted separately; only a few measurements made in the spring were available. These data are broadly similar to transparency data given by Powers et al. (1960), Verduin (1964), Hartley et al. (1966), and others. In general, summer transparencies in the range considered desirable for walleyes are found in the island and reef area; waters are more turbid to the south and west, and more transparent in all but the southwest corner of the Central Basin. All of these waters are more turbid in autumn, displacing the isoclines eastward. We emphasize that the isoclines are estimated means. The two isoclines depicted in Figure 5 enclose almost all the waters where walleyes have been caught regularly by both anglers and commercial fishermen in summer during recent years. Niagara Reef, still a reasonably good fishing ground in 1967, is just outside our estimated isoclines in an area for which we have relatively few data.

We have no evidence that these waters have become more turbid since 1900 except for a very recent increase due to channel dredging. Van Oosten (1948) found that turbidity had declined considerably in inshore areas along the south shore of the Central Basin but had not declined in the Western Basin (at Port Clinton, Ohio) during the first half of this century. The comparison of turbidity data published by various authors is made difficult by the number of methods used. Adequate tables to permit careful comparisons of existing data apparently have not yet been devel-

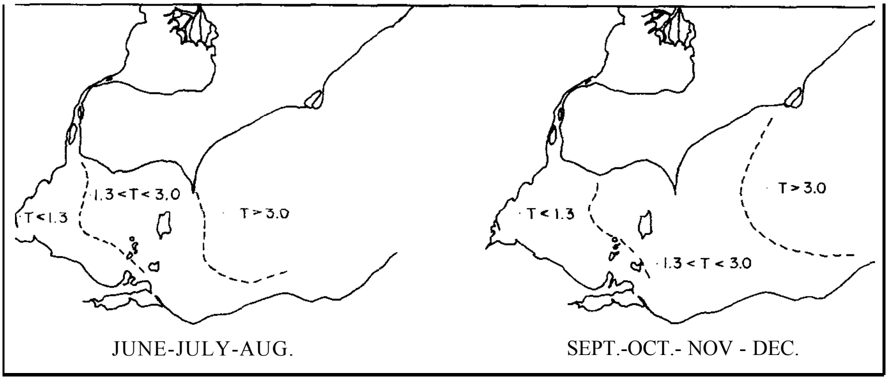

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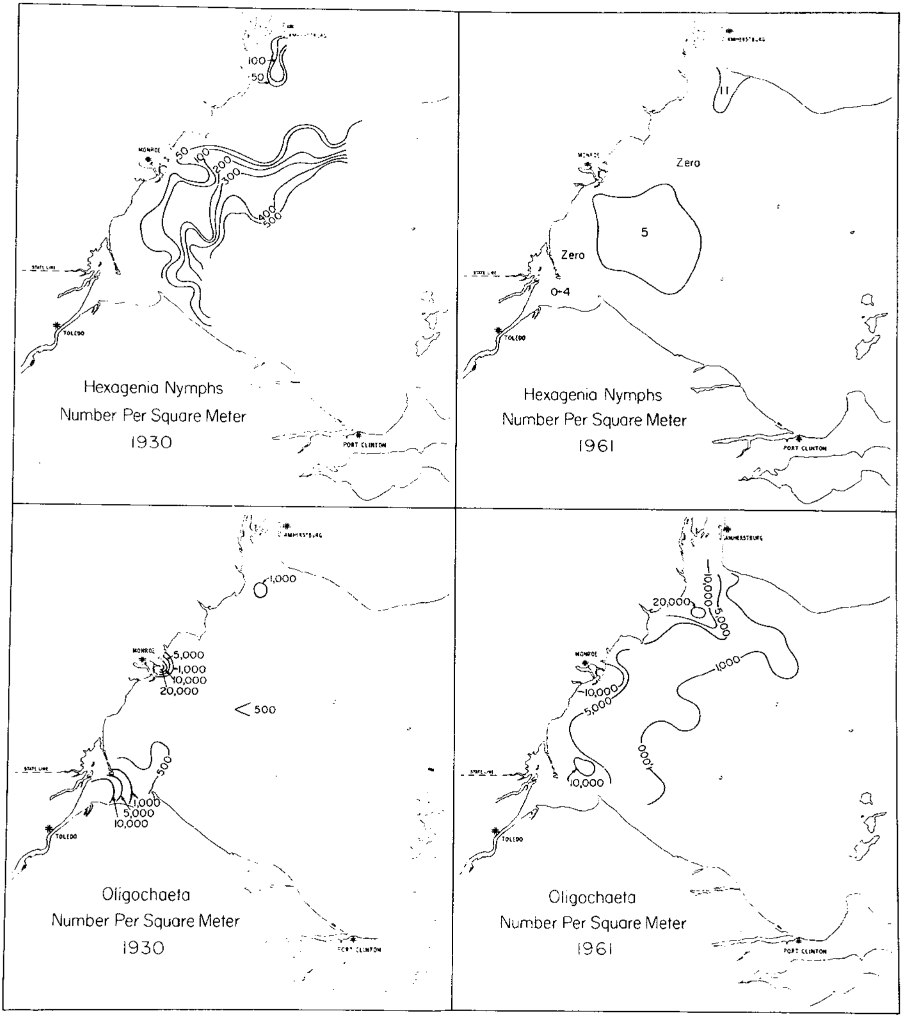
Figure 5. Estimated mean transparency isoclines in western Lake Erie, 1961-62-63. Data from Great Lakes Institute, University of Toronto. Isoclines are based on Secchi disc measurements expressed in meters.

oped. Generally, the recorded measurements of turbidity do support our view, stated in another section, that the waters along the south shore have apparently become somewhat more suitable for the walleye since the turn of the century. We doubt that whatever changes may have occurred in the relatively lower turbidity along the north shore will have influenced the walleye appreciably.

We have also suggested that some parts of the bottom of western Lake Erie have become modified during the past 150 years. Certainly the biota has changed markedly due to a complex of specific causes, all of which can be attributed to increased enrichment and pollution (Carr, 1962; Carr and Hiltunen, 1965; see Figure 6). We believe that sandy or rocky areas that have become muddy or overlain with "diatom fluff" are less suitable as resting locations for the walleyes due to the reduction in dissolved oxygen that occurs near these surfaces at certain times. M. Hosko (personal communication) and other fishermen state that the lake bed between Middle Sister and East Sister Islands, at depths of about 30 ft., was of relatively clean sand several decades ago but has become progressively covered with deposits of higher organic content as well as a "fluffy" material, presumably diatom skeletons. Walleyes once were taken regularly there in spring but have not been found in significant numbers in recent years. They can still be taken, however, in the vicinity of shallower reef areas which are "cleaner."

Whether the bottom in the Island Region has also deteriorated apparently has never been determined critically. Smith and Snell (1891) described a particular reef off North Bass Island as composed (circa 1885) of honeycombed rock interspersed with small patches of clay and sand "which are probably the best grounds for whitefish in Lake Erie. They extend 3-1/2 miles into the lake from the west side of the island, and on the north side they are about 5 miles square, running some distance into Canadian waters around the little group of islands known as Old Hen and Chicken."

A number of studies of the bottom deposits around the islands and Pt. Pelee have been made in recent decades (Kindle, 1933; Shelford and Boesel, 1942; Verber, 1957; Hartley, 1961; Wood, 1963). The boundaries drawn between various types of deposits *(e.g.,* between rock and mud) differ widely depending on the author. Despite these inconsistencies, the data suggest that the area of honeycombed rock around North Bass Island is not now as extensive as it was described some 80 years ago. A careful reconsideration of original survey data of recent studies might resolve the problem of whether these reefs of honeycombed rock are becoming, or have become, gradually silted-over. The fact that low oxygen concentrations have developed rapidly a number of times over broad areas of the bottom waters of the Western Basin only in recent


Hexagenia Nymphs Number Per Square Meter 1930

Hexagenia Nymphs Number Per Square Meter 1961

Oligochaeta Number Per Square Meter 1930

Oligochaeta Number Per Square Meter 1961

Figure 6. Comparative abundance of ***Hexagenia*** nymphs and Oligochaeta in western Lake Erie in 1930 and 1961 (from Carr and Hiltunen, 1965).

years (Carr et al., 1965), but not earlier, is consistent with the hypothesis that the organic content in the bottom deposits has increased and that "mud" deposits have become more extensive.

We suggest that bottom deposits with high organic content would act to reduce suitable walleye habitat, particularly in summer. What happens to walleyes during the periods of oxygen depletion in the Western Basin is not known. Presumably oxygen concentrations would remain higher over rock and clean sand than over mud. If not, the walleyes would most likely have to remain pelagic near the surface. This behavior would, of course, render them more susceptible to capture by "canned" gill nets.

On the basis of our knowledge of currents in western Lake Erie (e.g., Hartley et al., 1966) and sources of pollution, the earliest and still most rapid addition of nutrients and organic materials to bottom deposits has been along shore from Detroit to Toledo with lesser amounts to Catawba Island and between Windsor and Pt. Pelee. Areas least modified should be in the Middle Bass -North Bass-East Sister-Pelee Island waters. This pattern of deposition is also indicated by the types of benthic communities now persisting in these places when compared to those along the south and west shores (Beeton, 1961). It is in these least modified waters that walleyes persist in summer. As stated in another section, we judge from early records and the literature that some walleyes (perhaps predominantly the larger ones) once moved into the hypolimnion of the Central Basin in summer. These waters are now closed to them in the summer due to oxygen deficiencies.

Insummary, we judge that modification of bottom deposits along the shores, periodic oxygen depletion over extensive mud bottom areas in the Western Basin, and regular oxygen depletion in the hypolimnion of the Central Basin have reduced walleye habitat in summer.

Summer is the major growing period for walleyes; they grow little in winter (H. D. Van Meter, unpublished data). It is likely that a reduction of habitat in summer would eventually act to reduce a walleye population, especially if food were a limiting factor. There is no evidence, however, that the availability of acceptable food is limited. The walleye is, as stated in a preceding section, a generalized predator. It feeds on transforming mayflies and presumably did so in the Western Basin before the mayfly “doomsday” arrived in 1953 (Britt, 1955). Perhaps the greatest peak of abundance of the walleye in Lake Erie, at least in the past 150 years, was immediately after 1953, hence, we doubt that failure of this invertebrate prey population had much effect on the well-being of the walleyes. Great numbers of young fish of various species have been available in the “walleye waters” of western Lake Erie in recent years (V. C. Applegate and J. V. Manz, unpublished data) and there is no evidence that walleyes require anything other than suitable-sized fish for adequate nutrition. Thus, though we agree with Beeton (1966) that pollution has affected the walleye, we doubt that the major proximate cause of the decline in the population was the reduction of benthic food organisms.

We emphasize that we do not believe that a reduction in habitat (other than spawning habitat) in itself has been one of the major factors limiting the abundance of walleyes in recent times.

The high population densities that the walleye attained in western Lake Erie in the 1950's occurred under conditions that appear from all evidence not to have been substantially more favorable for the species than they were in 1967 - at least insofar as the extent of habitat and abundance of prey are concerned. Any critical alterations, in habitat particularly, that may have occurred apparently came before 1950 (Carr et al., 1965).

The observed growth rates of Lake Erie walleyes are among the most rapid ever recorded for this species [see data from 16 growth studies given by Payne (MS, 1964) and Table 5 in this report]. If, as Carlander (1948) pointed out, rate of growth is one of the most important indicators of the health of individual fish, then western Lake Erie walleyes recently have been extraordinarily healthy. On the other hand, we suggest that an unusual growth rate implies that the ecosystem is not healthy, i.e., it has not attained relative balance. We would expect the ecosystem to be healthier if the walleye population were larger and their growth rate were less, due partly to intraspecific competition for small perch, white bass, lake emerald and spottail shiners, alewives, etc.

Wolfert et al. (1967), who examined walleyes fromwestern Lake Erie for internal parasites, found that individuals commonly harbored a number of cestodes of the species *Bothriocephalus cuspidatus* in their pyloric caeca. No indication of inflammation was apparent. The walleyes with a greater than average number of cestodes were usually heavier, at any given length, than those with fewer cestodes. These parasites, and the few of another species that were present, seem to have had little effect on their hosts. A. Dechtiar (personal communication), who has periodically examined western Lake Erie walleyes for diseases and parasitic organisms in recent years, has always found some ill or infected fish, but has found no indication of serious infection or of widespread epizootics.

Dead walleyes have rarely been found on Lake Erie beaches in recent years, and fishermen seldom pick dead individuals off the bottom in their nets. Van Oosten (1936), who examined dead walleyes and other species washed onto the south shore, judged that they had been discarded by fishermen. Dead walleyes were common on the shores of Ohio islands in the early 1950's (Verduin, 1964). These, too, likely came from fishermen's nets. We have, then, no evidence of any serious outbreak of disease or parasites in Lake Erie walleyes, nor of any unusual mortality other than that due to human predation.

In a preceding section on the general ecology of the walleye, we indicated that natural mortality rates, corrected for concomitant fishing mortality, have been estimated for a number of walleye populations. In roughly comparable circumstances, these were found to be less than 10 percent per year for fish older than 1 year. We have no direct estimates of natural mortality rates for Lake Erie walleyes. On the basis of various considerations given above, we believe it to have been less than 10 percent in recent years.

Older walleyes often move freely under the ice in winter and feed actively; this is apparent from anglers' success when fishing with bait minnows. Doan (1945) summarized some local distribution and movements around the Ohio islands in winter. Forney (1966) gave circumstantial evidence that during periods of high abundance of adult walleyes and low prey availability, older walleyes prey on their own young-of-the-year during the winter. Such cannibalism is unlikely in western Lake Erie in recent years, however, because the young have been too large to serve the older walleyes as prey.

In summary, we judge that natural mortality of walleyes beyond the early fingerling stage is low in western Lake Erie and is not a major limiting factor in the abundance of the species.

Relative abundance of walleyes and interrelated species

As mentioned previously, various investigators have found that in waters suitable to both the yellow perch and the walleye, if one population becomes, and remains, markedly abundant for a number of years the other species is reduced in abundance. Theniches of perch and young-of-the-year walleyes are sufficiently similar that food shortage and competition may on occasion have a "competitive exclusion" effect. With predatory fish such as the larger percids, the role of predator and prey depends more on relative abundance and relative size of the organism than on any simple predator-prey relationship. We judge from considerable available data that the critical factor determining whether one percid will become the prey of another percid is more a matter of its being the right size and being available than of it being of a certain species. The dynamics of largemouth bass *(Micropterus salmoides)* and bluegill (Lepomis *machrochirus)* populations appear to be dominated by similar predatory interrelationships (Regier, 1963).

Lake Erie fishermen have enjoyed a fairly good market for perch as well as walleyes since about the turn of the century. Under such circumstances and with no important changes in fishing gear and methods, the total catch of the species is an approximate index of relative abundance. A marked change in fishing methods for walleyes after 1950 prevents us from using such an index for walleye abundance beyond that date (see next section).

According to catch records, perch were very abundant in the lake between 1929 and 1935 and again between 1954 and 1967 (Baldwin and Saalfeld, 1962, and more recent supplements; see Figure 7). Although catches by basins in Canadian waters suggest that perch were not markedly abundant in the Western Basin during the earlier period, we note that gill nets were not fished extensively in the Western Basin in those years and that the pound nets used were not very efficient for capturing perch (Davies, 1960).

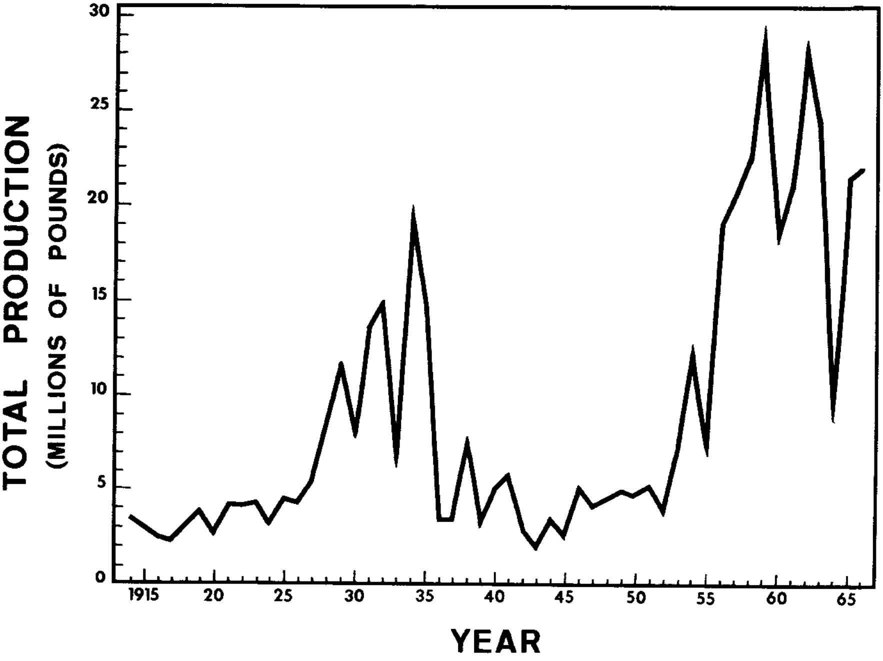


Figure 7. Commercial production of yellow perch in Lake Erie, 1915-66.

During the period 1928-35, when perch catches were high, walleye landings remained at, or below, average (Figure 8). After 1935, walleyes showed a rapid, two-fold increase in catch and then a gradual increase thereafter. The second great surge in the abundance of perch began in 1954. Abundance increased to unprecedented levels in 1956, where it has remained. Although walleye catches were high from 1953 to 1958, with a peak in 1956, evidence suggests that walleyes (in terms of mass and not numbers) were, in fact, most abundant in 1955 and only moderately abundant in 1950-53 and in 1957 (see next section). After 1957, the walleyes fell to low levels of abundance while perch maintained themselves in great numbers.

White bass were very abundant in the Western Basin in some early years. According to Smith and Snell (1891), this was the most abundant species about 1825 to 1835; they were caught again

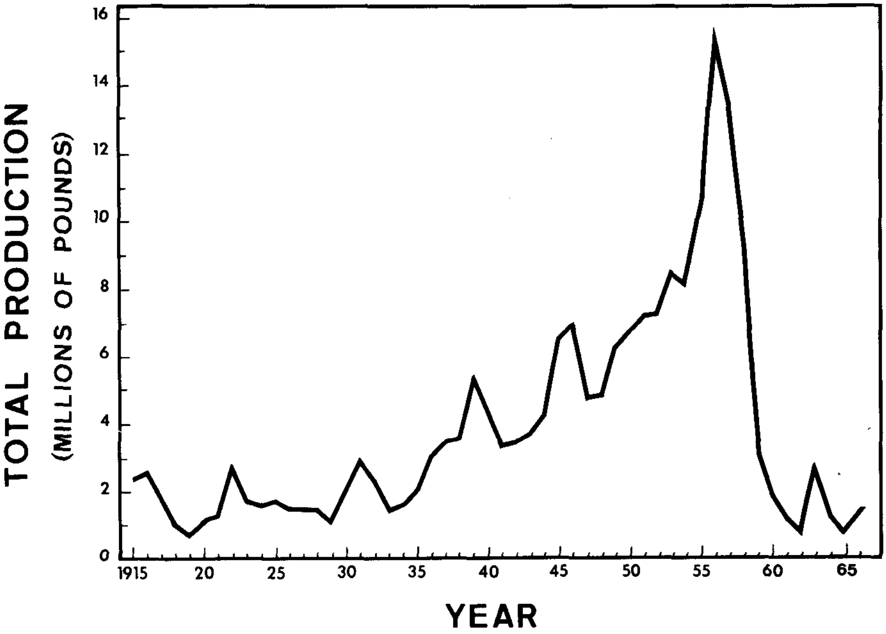


Figure 8. Commercial production of walleyes in Lake Erie, 1915-66.

in "immense quantities" between 1853 and 1860. These authors commented that the white bass and muskellunge decreased more rapidly than any of the other species in the lake. We suggest that the major reasons for the decline of the white bass were the combination of increased turbidity and the increased abundance of the *Stizostedion* species. Catches of white bass increased moderately from 1928 to 1935, then declined and returned to prominence in western Lake Erie beginning about 1953. We do not know what the predator-prey interrelationships are, but expect that the larger walleyes eat young-of-the-year white bass when other food is scarce. J. L. Forney (personal communication) has found that walleyes eat white bass in Oneida Lake, but noted that relatively rapid growth of white bass tended to reduce predation on them. Various reports indicate that minnows and other small pelagic fish were scarce in offshore areas of Lake Erie some decades ago; conversely, forage minnows have increased substantially in numbers since 1959 (U. S. Bureau of Commercial Fisheries trawl data).

The very successful year classes of perch and white bass in 1951 and 1952 when walleyes were relatively abundant are difficult to explain. Young-of-the-year of both species are caught in large numbers just above the thermocline in the Central Basin, especially in the western part. As indicated previously, we believe that both the blue pike and walleye, except during the pelagic fry stage, were barred effectively from most of the Central Basin beginning in the late 1940's by low oxygen levels in the hypolimnion in the warmer months. The years 1951 and 1952 may have been the first ones after the late 1940's in which conditions were suitable for a very successful hatch of perch and white bass. The Central Basin sanctuary would tend to ensure their survival through the critical young-of-the-year stage. Abundant yearlings of perch and white bass (as well as smelt around the margin of the Central Basin), would have provided more than enough food for the walleyes, thus permitting a higher than normal survival to age II when size makes both species generally invulnerable to predation by the walleye. A shrinking habitat for the relatively sedentary walleye in summer would also act to protect the more mobile, more pelagic young and yearlings of perch and white bass.

Finally, 1951 marks the beginning of the sharp increase in Ontario's catch of walleyes in the Western Basin, for reasons given in the next section. The sanctuary that the walleye had enjoyed in Canadian waters was lost with the introduction of new fishing methods. Cropping these fish relieved the predatory pressure on perch and white bass improving their survival. J. L. Forney (personal communication) has noted that yellow perch, white bass, walleye, smallmouth bass, and gizzard shad (Dorosoma *cepedianum)* produced exceptionally large year classes in Oneida Lake in 1954. It seems unlikely to him that environmental conditions could have been exceptionally favorable for reproduction of all these species. The shad appear to be preferred prey for the walleye and may have acted as a "buffer" that permitted unusually high survival of other species (Lagler and Applegate, 1943; Wolfert, 1966).

We conclude this section with the admission that it is a crude analysis but we are convinced that it provides more than sufficient evidence that the commercial catch data do not contradict the ecological model that we have presented.

Introgression and desegregation

Earlier we suggested that introgression among *Stizostedion* forms played a role in the disappearance of blue pike and sauger in Lake Erie. The term introgression is used here in the sense of desegregation among two or more gene pools that had previously remained largely discrete for reasons other than simple spatial barriers. A process of desegregation between two forms can have various kinds of outcomes such as: one or both of the old forms become modified somewhat; one new form is added to the two earlier forms; one of the earlier forms remains, with a new composite form added; both earlier forms are replaced by a single composite form; one or both of the old forms disintegrate with no composite formed; or, both old forms and any composite form disintegrate. The second from the last possibility, i.e., disintegration of several of the old forms with no composite formed, is the one we postulate to have occurred among the *Stizostedion* species in Lake Erie.

Having specified some possible outcomes of a desegregation process, we now consider the "risk" or possible advantage to the joint ecological position of the taxonomic products of such a process when compared to the combined ecological status enjoyed by the old forms. It is not difficult to postulate instances where the net effect could be advantageous (Butler, 1968), although the effect most often appears to be deleterious (Stebbins, 1966). To clarify the idea somewhat, and place it in a practical frame of reference, we present a simple model of the "risk" and possible advantage in the desegregation process, in which risk is expressed as a function of the degree of dissimilarity between gene pools of the desegregating forms. The degree of dissimilarity would have to be inferred from phenotypic differences; precisely how these differences could be quantified remains a problem.

Figure 9 depicts a model of risk consistent with our understanding of the desegregation process. To obtain objective estimates of curves such as these would require data on the outcomes of a substantial number of desegregation events with corresponding gene pool dissimilarities measured in comparable units. Following is a brief statement of aspects of the model.

We suggest that the probability that interbreeding between the two forms will reach general proportions, P(interbr.), in the absence of spatial barriers, starts with a value of 1 when gene pool dissimilarities are 0, then descends as a sigmoid function of increasing dissimilarities (Figure 9a). If such interbreeding occurs, we suggest that the probability that it will have a net deleterious effect, P(delet.), is 0 at a level of no dissimilarity, rising as a sigmoid function and reaching 1 asymptotically but at somewhat lower levels of dissimilarity than with the preceding function (Figure 9b). The probability of net advantage is simply the mirror image of the preceding function, P(advant.) = 1 - P(delet.). If interbreeding has occurred and if it has had a deleterious effect, we postulate that the negative measure of the effect, D, is 0 at a level of no gene dissimilarity, but decreases approximately exponentially as dissimilarities increase (Figure 9c). On the other hand, if desegregation has occurred and the effect, A, has been advantageous, we postulate that the effect is 0 at no dissimilarity, rising to a modest peak at low levels of dissimilarity (where a new form exhibiting general hybrid vigor may be produced) and then gradually falling off (though remaining positive due, perhaps, to advantageous effects of introgression where one form has "swamped" the other, or where genetic desegregation has remained on a small scale thus providing a small source of new genes for one or both pools) (Figure 9c).

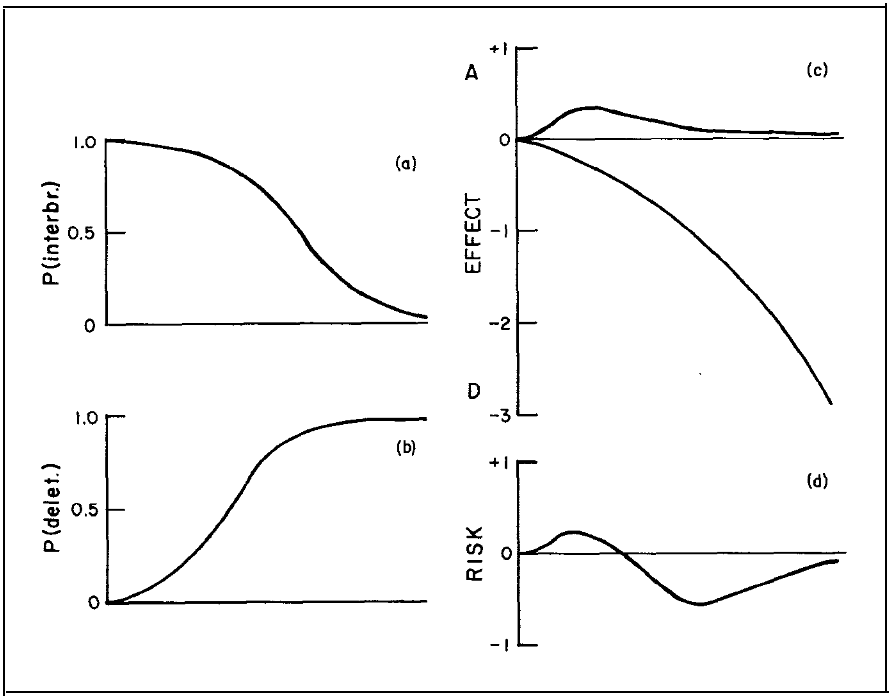


Figure 9. Model of risk from a desegregation process. Abscissae are: in each case, a measure of gene pool dissimilarities.

An effect, C, is associated with the probability of non-desegregation, P (non-interbr.), and the C is taken as 0 to be consistent with other definitions above.

Our simple model to describe the effects we expect of desegregation, i.e., the risk is as follows:

$$\text{Risk} = [P(\text{interbr.})][P(\text{delet.})][D] + [P(\text{interbr.})][P(\text{advant.})][A]$$

$$= P(\text{interbr.})[A - (A+D)\ P(\text{delet.})]$$

From the practical viewpoint, the risk is the expected impact on the joint status of the relevant forms in the community, where status is measured, *e.g.,* in units of long-term yield to fishermen. We expect that the net impact of desegregation (advantage minus disadvantage) will be positive at low levels of gene pool dissimilarity, since the new gene pool will exhibit a moderate increase in heterogeneity which will produce genotypes pre-adapted to the changed conditions that triggered the interbreeding. At higher levels of gene pool dissimilarity, corresponding, e.g., to differences between sibling species, the expected impact will be negative as is generally the case with "hybrids". We then expect the net impact to become less pronounced as the probability of desegregation approaches 0, corresponding to a degree of dissimilarity existing between species of longer standing (Figure 9d).

We repeat that we have no numerical data with which to test the above model. Its features are consistent with what little we do understand about these processes, in fish communities. We propose it not solely for the purpose of formulating a new theory, but rather to indicate the context in which we approach the following discussion.

The degree of genetic difference between blue pike and walleyes has never been measured satisfactorily. Deason (MS, 1936) and Stone (MS, 1948) studied the taxonomic status of the walleye and blue pike in Lake Erie (Stone also examined a pair of similar forms in Lake Ontario); both were unable to distinguish between all individuals on the basis of morphometry. Since Deason's concept of a species rested heavily on morphometric differences, he considered the two forms to be subspecies of the same species. Stone (MS, 1948), who used Mayr's "biological species" concept (restated in Mayr, 1963), and data collected in the 1940's found that the forms differed markedly in growth rate, maximum size, age at sexual maturation, location and time of spawning, and food habits. He decided that they were isolated reproductively and, therefore, separate sibling species.

C. F. Clark (1959) experimentally crossed walleyes and blue pike from Lake Erie at the Put-in-Bay Hatchery in 1955. Reciprocal crosses led to viable young, although the hatch of walleye male x blue pike female was much lower than the reverse. At the end of the first summer, all of the walleye male x blue pike female offspring had apparently died; some of the offspring from the reciprocal cross survived to age I. None were captured after their second year of life, consequently it is unknown whether these progeny were sterile.

What is the evidence of hybridization and gene exchange between Lake Erie's blue pike and walleye populations? Early writers occasionally referred to the "gray pickerel" as intergrades between the blue pike and walleye (Goode, 1884). Whether they had anything other than circumstantial evidence upon which to base this hypothesis is not known. Deason (MS, 1936) found slightly lesser morphometric differences between the blue pike and walleyes caught near the traditional. walleye areas than between those separated by a greater distance. He took this as evidence of some genetic exchange. Stone (MS, 1948), other biologists, and many fishermen have found individuals that appeared to be hybrids both in morphometry and color. According to reports from some fishermen in eastern Lake Erie, unusually large fish resembling the blue pike appeared to be sterile. These fish were caught during the years following the almost total collapse of the blue pike population in that area of the lake. An occasional "blue" or "grey" form is still reported caught in Lake Erie. Three specimens collected in 1967 and submitted to the Royal Ontario Museum of Zoology, were identified as walleyes (W. B. Scott, personal communication).

Bluish-coloredwalleyes are, at present, common in some northern Ontario lakes. This color is due to the blue mucus which partially shields the more normal yellow pigmentation of the chromatophores.

Introgression among fishes might occur in several ways. If a mobile species or form becomes very abundant in its preferred habitat, population pressures may force it into marginal habitats. These unusual wanderings may interfere with whatever memory or instinctive mechanisms lead the animal to a suitable spawning site. It may then, at spawning season, become "trapped" by spawning schools of related forms and interbreed. An instinct to form schools and spawn at such times might override instinctive barriers to the strange species. Svärdson (1953) noted this behavior with some coregonids. Smith (1964) has found evidence that the deepwater chubs in Lake Michigan, a complex of Coregonid forms, have undergone hybridization and introgression during recent decades.

We also hypothesize that if forms that typically gather in large schools at spawning time become so scarce that schools remain small, these schools may fuse with schools of a related form.

We can speculate further that our *Stizostedion* forms may be imprinted by a characteristic bouquet due to some biotic components of a reef or gravelly stream system (Hasler, 1966). Some significant essences of the bouquet may be lost suddenly through rapid pollution or eutrophication which causes the extinction of those organisms whose metabolites contribute to the bouquet. Lacking adequate cues for orientation, sexually ripe adults may wander, become trapped in other schools of spawning fish of a related form and hybridize.

We do not know whether interbreeding of this kind occurred with the walleye and blue pike. The evidence suggests that these were sibling species, and that hybrids occurred but were sterile. Blue pike spawned in the deeper waters of the Central Basin about 2 weeks later than did the walleye (Deason, MS, 1936). Whether walleyes trapped in schools of blue pike, in the somewhat cooler waters, would ripen at approximately the same time as blue pike, or vice versa, is not known.

The destruction of spatial isolation between the blue pike and the walleye very likely resulted from the movement of walleyes from the Western Basin into the Central and Eastern Basin during their great abundance in the 1950's (Ferguson, 1957; Davies, 1960). Furthermore, the inferred stress of increasingly large areas of anoxic waters in the Central Basin probably displaced the blue pike into waters frequented by the walleye (Carr, 1962). Given violently fluctuating stocks (caused by an opportunistic fishery), the juxtaposition in time of abundance of one form and scarcity in the other, the model of risk specified earlier, and the limnological and behavioral inferences already stated, we see a likelihood that genetic desegregation did play a role in the final disappearance of the blue pike. We suggest, however, that this was a "mopping up" phase of the disintegration of the blue pike population already under great stress by man the predator and man the polluter.

The sauger in Lake Erie has attracted little scientific attention, and is now almost non-existent. Natural hybrids between the walleye and the sauger have been seen in other waters by only one observer (Stroud, 1948). Trautman (1957) suggested that similar hybrids may occur in Ohio. Nelson, Hines, and Beckman (1965) hybridized walleyes and saugers and found that the female sauger x male walleye yielded no surviving fingerlings; the male sauger x female walleye did yield some, though relatively few, healthy fingerlings. Uthe, Roberts, Clarke, and Tsuyuki (1966) found a number of types in the electrophoretic patterns of Lake St. Clair walleyes; one type closely resembled that of the sauger. At first glance this could indicate introgression. However, analysis 0 f electropherograms from other Ontario populations of *Stizostedion* species suggests that conventional electrophoretic patterns may not be sufficiently diagnostic to distinguish between them, much less to identify any intergrades (Ontario data).

Saugers and walleyes apparently migrated to the same or closely contiguous areas of western Lake Erie to spawn, e.g., in the Maumee Bay-Maumee River area. Reproductive isolation probably was maintained by somewhat different spawning sites and spawning periods although how these might have differed is not known. If desegregation occurred between saugers and one of the other forms (probably the walleye, if any), it appears to have been an occasional or gradual process. This, we must emphasize, however, is even more speculative than with blue pike.

In terminating this discussion, we wish to register our expectation that introgression and desegregation will be found to be far from rare in rapidly transforming systems once ecologists start looking for the necessary evidence. Freshwater systems under massive attack by man, as the Great Lakes are today, should provide evidence of numerous phenomena of this kind (see Regier, 1968, for further discussion).

THE WALLEYE FISHERY OF WESTERN LAKE ERIE

In an earlier section, we described the development of the commercial fishery in Lake Erie, fluctuations in the catch since 1900 (which we ascribe to an imbalance caused by heavy fishing), and finally the disappearance of a number of species in which other factors (environmental change, introgression, . . .) played some part.

Since 1880, the fishing industry in the United States, and more particularly in Ohio, enjoyed a large measure of freedom. Technology improved and the fishery became highly exploitive. Only in the last decade of declining catches have restrictions become severe and technological improvements static. During the last century and the early part of this century, the less heavily fished Ontario waters served as a sanctuary and helped sustain the fishery. If Ontario fishermen had had ready markets and been given the same freedom as United States fishermen, we suspect that the violent fluctuations and decline in valuable species would have come much earlier. The distribution of fishing pressure has reversed in the last 20 years. Commercial fishermen in Ontario, given almost complete freedom of action, have maintained relatively high levels of production of available species by improving fishing methods and increased fishing effort, while fishing in the United States waters of Lake Erie has declined.

Although we will now examine in detail the effects of heavy fishing for walleyes mainly by Ontario operators in the last 20 years, we must reiterate that heavy fishing in the United States earlier contributed to the instability of Lake Erie fish populations and indirectly to the decline of the walleye in recent years.

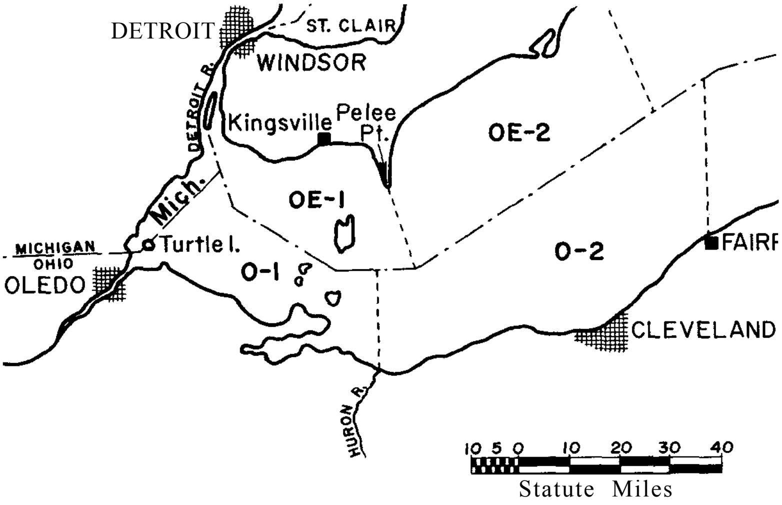
Efforts, catches, and technology

The total annual catch of walleyes in the period 1945-66 is shown in Table 2. These data extend, in both time and degree of detail, the available summaries for western Lake Erie from Ohio (Cummins, 1956), Ontario (Davies, 1960), and for Lake Erie by political subdivision (Baldwin and Saalfeld, 1962).

For approximately a century, Ohio exploited the walleye in varying degrees but recently with only a moderately intensive fishery. Walleyes were taken in large numbers in Ohio waters of

Table 2. Total commercial landings of walleyes by year from western Lake Erie waters, 1945-66. [Data not available for some early years. Pertinent statistical districts given parenthetically below state and provincial names; geographic boundaries of these districts are shown in figure beneath table (from Smith et al., 1961)]

Year	Michigan (Mich.)	Ohio (0-1)	Ontario (OE-1)	Total
1945	251,921	2,685,275		
1946	494,026	4,190,467		-
1947	348,421			
1948	402,908	2,580,743	184,522	3,168,173
1949	357,995	3,679,259	279,587	4,316,841
1950	330,941	3,594,737	339,022	4,264,700
1951	247,813	3,710,797	726,179	4,684,789
1952	285,130	3,035,771	1,296,011	4,616,912
1953	383,451	3,632,001	1,206,447	5,221,899
1954	221,239	3,223,692	1,657,087	5,102,018
1955	227,437	3,760,152	3,230,995	7,218,584
1956	234,524	3,837,400	5,366,628	9,438,552
1957	288,509	2,841,265	4,854,799	7,884,573
1958	292,381	3,060,555	2,865,957	5,218,701
1959	129,189	653,127	803,849	1,586,165
1960	102,536	715,602	548,929	1,367,067
1961	105,094	385,745	207,770	698,609
1962	52,912	196,606	210,941	460,459
1963	93,047	431,800	1,251,087	1,775,934
1964	121,481	265,433	475,016	861,930
1965	86,756	203,703	282,100	572,559
1966	76,100	107,684	727,513	911,297



both the Western and Central Basins. Ontario, until recently, had Only a small fishery with most of the catch coming about equally from the Western and Central Basins; this fishery became much more intensive about 1950. Thereafter, Ontario took increasingly larger catches, which reached a peak in 1956 that coincided with a record high production of walleyes in the United States waters of the Western Basin. Catches in all areas then fell somewhat in 1957, declined abruptly in 1958, underwent an equally severe drop again in 1959, and have remained at a low level since.

This increase of annual catches was offset approximately one year in the Eastern Basin where the peak harvest was made in 1958. This delay, together with data on tagged fish moving eastward during the somewhat higher population densities of the mid-1950's, leads us to suspect that during some of these years there was a migration, perhaps one-way, of walleyes from west to east into regions of lower population density.

To explain what was responsible for the change in catch, and the effects of the catches on the stock, we must consider changes in netting material, manner of fishing the nets, changes in total effort, changes in seasonal distribution of the effort, and changes in the relative abundance of walleyes. The gill net fishery is considered first.

In Table 3, we present data on effective effort and catch per unit effective effort from 1948 to 1961 for various gears and political subdivisions of the Western Basin (see Hile, 1962, for criteria determining effective effort). We use these data more for shedding light on the results of improving gear and methods than on determining walleye abundance. We judge that catch per unit effort from Ohio's trap net data is the least biased of all the estimates of the relative abundance of walleyes for that period when they are vulnerable to the gear. Gill net data on effective effort are seriously underestimated for reasons we now outline.

Nylon mesh in gill nets was used experimentally in small quantities by fishermen in Lake Erie in 1948. They compared catches made with nylon and cotton or linen and generally found nylon to be several times as efficient as the older materials (Van Oosten, 1949). The relative efficiencies of nylon and cotton nets have been tested for various fishes by a number of investigators (see e.g., Atton, 1955). For the walleye, nylon was estimated by Atton to be 3.2 times as efficient as cotton in relation to weight of catch with small mesh sizes (2 in. stretched measure), but only about 1.5 times as efficient for large mesh sizes (5 in. stretched measure). These estimates agree closely with other available estimates, some of which were cited by Atton. Nylon nets had an additional advantage since they did not require drying between lifts and could be fished continuously.

Table 3. Effective fishing effort and catch per unit effort for gill nets, trap nets and pound nets fished in western Lake Erie (District O-l and OE-1), 1948-61.

(No adjustment made for change in gill net mesh and methods; CPE for gill nets - pounds per thousand yards; CPE for other gear - pounds per lift)

	Province of Ontario								State of Ohio	
	Small-mesh gill nets		Large-mesh gill nets		Pound nets		Trap nets		Trap nets	
Year	Millions of yds. lifted	CPE	Millions of yds. lifted	CPE	Lifts in thousands	CPE	Lifts in thousands	CPE	Lifts in thousands	CPE
1948	2.9	8.4	1.6	13.6	8.4	16.4	---	---	69.7	35.0
1949	2.7	10.3	1.4	59.5	8.9	18.9	---	---	82.0	43.6
19 50	6.8	16.2	1.6	65.8	6.1	18.8	0.3	30.0	68.9	44.6
1951	10.9	24.7	2.4	104.2	4.7	15.7	2.8	48.1	76.0	43.9
1952	14.9	37.4	6.8	61.2	1.9	18.6	5.9	44.4	76.7	35.3
1953	8.7	18.7	7.2	98.8	5.4	9.8	5.0	56.7	70.2	51.7
1954	12.6	24.4	7.1	137.0	3.2	16.2	5.9	55.5	70.7	45.5
1955	11.2	63.4	9.4	221.8	2.3	20.4	4.4	86.3	53.8	67.1
1956	10.2	125.2	11.0	335.6	3.4	9.3	6.8	56.9	50.5	67.7
1957	14.2	111.1	11.0	277.6	3.0	8.1	5.4	37.1	46.8	52.0
1958	17.4	42.4	10.0	192.0	2.4	3.2	4.5	26.8	41.5	41.2
1959	7.8	21.6	6.1	100.8	1.5	1.7	2.5	9.1	27.2	15.8
1960	15.1	21.6	2.3	77.8	1.5	8.3	4.3	5.1	26.2	18.2
1961	10.5	11.5	1.2	55.6	1.0	2.8	1.9	7.7	65.7	4.3

By 1950, considerable amounts of nylon gill netting were fished in the Ontario waters of Lake Erie, and the change from cotton to nylon was essentially completed by 1952. The number of yards of gill nets licensed in Ontario's Western Basin during the period 1951 to 1954 was about 25 percent less than that of the preceding 5 years. After 1954, the licensed yardage increased rapidly to about twice that of the immediate pre-nylon period and has remained at approximately that level. Since almost all of Ontario's gill netting in the Western Basin after 1961 has been with small and intermediate mesh, it is apparent that the potential effort had increased about 5-fold between 1949 and 1961, assuming an increase in net efficiency of 2.5 and a doubling of yardage fished.

Several additional technological changes must be taken into account. Ontario fishermen re-introduced and gradually elaborated the technique of floating or "canning" nets near the surface to intercept walleyes and other species that migrated or foraged at intermediate depths. This method was used in the 1940's (W. B. Scott, personal communication) and became general in the early 1950's. Canning greatly increased the efficiency of gill nets for catching walleyes and white bass, according to all reports, but direct estimates of this increase are lacking.

Whether the amount specified in the license in any way deterred the fishermen from fishing more gear than that to which he was legally entitled is not known. No attempt to restrict Ontario's Lake Erie fishermen to the licensed amount has apparently been made since at least 1950. Some reports state that there was, in fact, no relationship between gear licensed and gear fished about 1950. In addition to greater quantities of large mesh nets fished, there was a marked increase in the small mesh netting (2-1/2 to 3-1/8 in.) during the 1950's. Intermediate mesh netting (3-1/4 to 4-1/4 in.) was permitted by Ontario in 1962 and subsequent years. The approximate selectivities of these gears are shown in Figure 10.

The estimates presented in Figure 10 were obtained from data for the walleye taken in randomized sets of a graded, gill net series in Saskatchewan lakes (courtesy of F. M. Atton). The estimates were obtained by using graphical method Number 2 and Type B selectivity curves given by Regier and Robson (1966). Data taken in similar manner in western Lake Erie by Ohio are not sufficiently extensive for both small and large walleyes to permit the computation of estimates. The Ohio data were sufficient, however, to perform an informal test of the accuracy of the estimates in Figure 10. We conclude from this comparison that the selectivity curves of various mesh sizes for the walleye of western Lake Erie would be offset perhaps 5 to 10 percent to the left of those shown in the figure. This difference may be due to a greater plumpness of the Lake Erie fish.

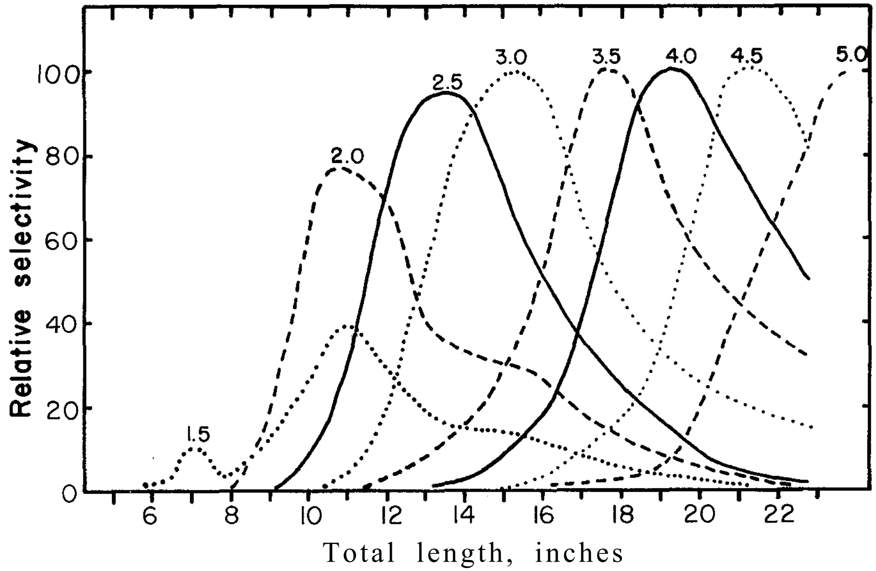


Figure 10. Selectivity of nylon gill nets of various mesh sizes for walleyes. (Mesh sizes given in inches at peaks of curves; data provided by F. M. Atton).

Whereas the large mesh sizes (4-1/2 to 5 in.) would normally take relatively few walleyes under 17 in. (total length), the intermediate meshes (3-1/4 to 4-1/4 in.) are quite effective in taking fish down to about 13.5 in. and the small mesh nets (e.g., 2-1/2 in.) in capturing those down to 11 in. The small meshes are now regularly fished for perch but were used extensively during the 1950's for the walleye; the intermediate mesh, originally intended for white bass, has come to be known as the "pickerel" (Le., walleye) mesh.

In the 1940's, Ontario fishermen set large mesh nets in the Western Basin for walleyes almost exclusively in March, April, November, and December. Subsequently, in the early 1950's these nets were "canned" to fish near the surface. Fishing was also extended into the summer since the new nylon gill nets would not rot. Although the largest share of the gill net catches during the 1950's were made with large mesh nets, very considerable quantities were taken by small mesh nets. The latter gear was fished most intensively during the summer.

Since 1962, the new intermediate mesh gill nets (or "pickerel" mesh) have been used largely in late spring and early fall. The nets are set to intercept both walleyes and white bass, since the combination of the two species is profitable. Until the autumn of 1966, little official concern was expressed over the fact that many of the walleyes taken by this fishery were small-between 13 and

16 in. (total length). Fish of this size were much in demand and were disposed of commercially with little difficulty. In the autumn of 1966, large numbers of small walleyes were taken by this fishery. The Ontario government tried to enforce the minimum size limit (14 in., total length) by court action.[10] Informal reports indicate that the practice was not halted, though its scope may have been reduced. At any rate, the catches went unreported. Some informal reports indicate that the actual catch in the autumn of 1966 was about three times the officially reported catch.

Because of the sequence of circumstances outlined, we do not know how to arrive at reasonable estimates of the effort, in terms of truly comparable standard units, expended during individual years of the past 2 decades. We suggest that in some years in the 1950's, fishing effort for walleyes in Ontario was about 50 times greater than in the late 1940's.

By way of comparison, the effective effort expended by Ohio's major gear, the trap net, decreased regularly from a peak in 1949 (Table 3). Technologically, the trap net fishery did not change appreciably during this period. It remained a spring and fall fishery.

Ontario's pound net fishery decreased more or less regularly from a peak in 1949. Conversely, about 1949, the Ontario trap net fishery expanded rapidly to a peak in 1956 but has declined considerably since then. Even in 1956, Ontario fishermen operated less than 10 percent of the number of trap nets used by Ohio fishermen in the Western Basin.

The Ohio gill net fishery also expanded substantially during the 1950's. In general, the statements made about gill net fishing in Ontario apply to Ohio's operations as well. Michigan's small catches have been taken almost exclusively in trap nets since 1950. Other gear used recently in the Western Basin (hooks, Ohio's fyke nets, sturgeon nets, etc.) have taken few walleyes. The sport fishery is pursued largely in Ohio waters and the catch during the past decade has been almost negligible in comparison to the commercial landings (Keller, 1964, 1965). Much larger catches were reportedly made in the 1950's, but it seems unlikely that these would have exceeded more than 5 percent of the commercial catch.

The general picture, then, is one of a walleye fishery dominated for decades by the Ohio trap netters. Beginning in 1948, a change to nylon netting, the canning of gill nets, increasing amounts of gear set, and a laissez-faire management policy permitted gill netters, particularly in Ontario, to increase their effectiveness in

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[10] From 1937 to 1954 Ontario's minimum size limit for walleyes was 15.0 in., fork length, which is equivalent to 16.0 in., total length. In 1954 the limit was dropped to 14.0 in., total length.

taking walleyes about 50-fold. Large catches were made for a few years. Contemporaneously, a series of changes occurred in the abundance of various fish species (smelt, yellow perch, white bass) in the ecosystem. The walleye population collapsed in 1959 and large walleyes have been scarce consistently since that event.

The “fishing-up” of the walleye

It has been suggested sometimes that the great peak in walleye catches during the 1950’s was due to one or two enormous year classes that arose as a result of unusually good spawning conditions. There is, however, no evidence of exceptionally strong year classes in samples of walleyes taken from the U.S. trap net fishery. Instead, this high production appears to be an instance of “fishing-up” the resource as described by Ricker (1961).

The walleye of western Lake Erie shows the following typical stages, viz.:

(1) Compared to most earlier years, success of reproduction appears to have increased greatly during the 1940’s when Ohio’s catches were gradually increasing;

(2) Growth rate has also increased markedly (Figure 11), presumably as older fish were removed; and,

(3) Although we have no data demonstrating an improvement in survival as postulated by Ricker, we believe from indirect evidence discussed earlier that natural mortality is less than 10 percent per year.

Population numbers and mortality rates

Currently available data do not yield direct estimates of population numbers and mortality rates (natural, fishing, or total) for the walleye population of western Lake Erie. Commercial catch statistics and data from periodic samples of the landings permit separation of reported catches in various periods into numbers of fish by age group and year class. These data can then be analyzed by using catch curve models and methods to yield approximate measures of total mortality rates (see Ricker, 1958). Table 4 shows the estimated numbers of fish contributed by the 1960 to 1966 year classes to the catches of walleyes in western Lake Erie in 1962 through 1966. It proved impractical to summarize comparable information for the years before 1962. The data in Table 4 are not highly accurate because adequate samples of catches could not be obtained from the many types of gear, fishing areas, and landing ports in the limited sampling carried out by the agencies involved.

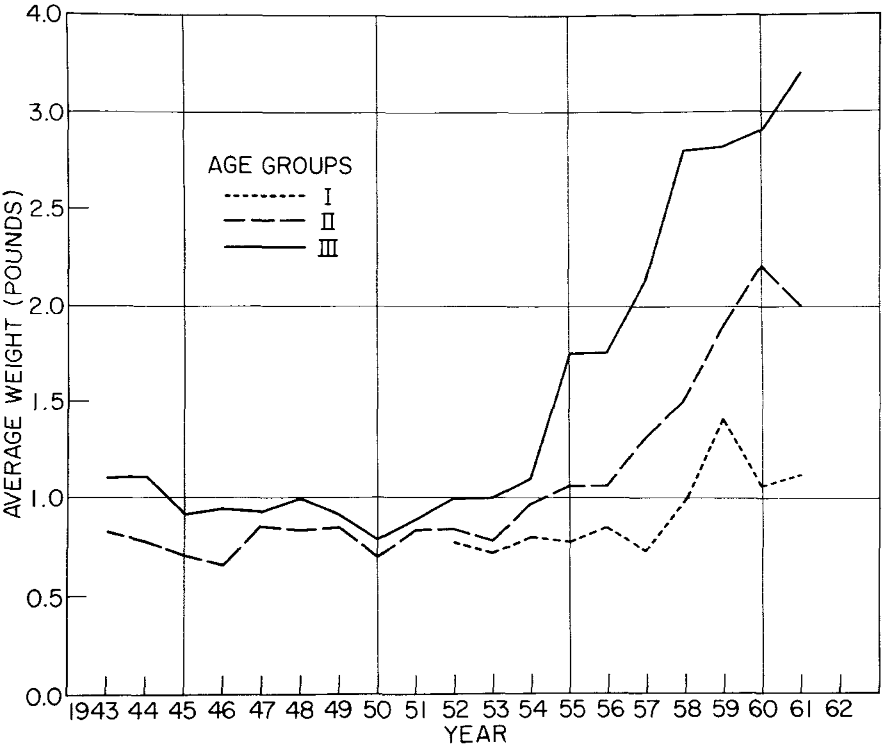

Figure 11. Mean weight of walleyes of age groups I-III (sexes combined) insamples of commercial landings taken from the Western Basin, 1943-61. (From Anon., 1963; mean weights of similar mid-autumn samples combined for the entire period 1962-1966 are given in Table 5 for fish indicated there as I+, II+, and III+.

Suitably detailed data on catch per unit of effort are conventionally used for estimating total mortality by catch curve methods. We face several difficulties in trying to interpret the catch per unit of effort statistics for western Lake Erie walleyes as measures of abundance.

A model used frequently to estimate mortality rates of fish subject to commercial exploitation for an extended period states that catch per unit effort is equal to the product of the Poisson catchability coefficient and the mean population size during the period in which the catch was made (Beverton and Holt, 1957, p. 234 ff.; Regier and Robson, 1967).

First, we note that according to this model catch per unit effort (whether "corrected" or not) is a function of mean population size. The greater the proportion of fish taken out in a particular season, the further the mean would be from the original number at the beginning of the season. Presumably the latter parameter would be of primary theoretical interest.

Table 4. Estimated numbers of walleyes of various year classes caught by the combined fisheries of Ohio, Ontario, and Michigan in Western Lake Erie, 1962-66.

Catch in year	Contribution to catch by year class						
	1960	1961	1962	1963	1964	1965	1966
1962	19,145	154,940	32,162	-			
1963	1,260	189,761	1,644,585	91,770			
1964	5,764	42,064	536,173	25,343	1,389		
1965	1,076	11,862	197,182	48,967	80,991		
1966	0	245	6,815	28,305	157,769	703,4721	0[1]
Totals	27,245	398,872	2,416,917	194,385	---	---	---

*Figures probably seriously underestimated according to rumors of widespread non-reporting of undersized walleyes taken in Ontario waters in these years.

Secondly, the catchability coefficient depends not only on how good fishermen are in locating the fish, but also on how the size selectivity of the gear is related to the length-frequency distribution of the species taken. Thus, the catchability of 3-in. gill nets for 15-in. long walleyes would be much higher than for 10- or 20-in. walleyes. The year-to-year catchability coefficient of 3-in. mesh would vary with the size-frequency distribution, the latter depending to some extent on the history of exploitation suffered by the individual size classes present.

It would be possible to simulate a particularly well-understood fishery, in which only year-class strength and amounts of gear fished varied from year to year, on an electronic computer to provide some idea of the functional relationship of catch per unit effort to abundance. This we have not attempted for it appears to us that annual catch alone as listed in Table 4, uncorrected for effort, is as acceptable a statistic for the estimation of mortality rate as any that we might derive from available data. The explicit assumption that walleyes have been in sufficient demand in recent years to cause a constant high effort to be expended against them, would also permit direct use of catches as listed in Table 4 for estimating total mortality rates from catch curves. In adopting this approach, we are simply being prudent and realistic with respect to adequacy of data, suitability of model and method, and reliability of the resulting estimates.

Catch curve analysis of the data in Table 4 indicates that total mortality rates for walleyes in the period 1962 to 1966 have averaged about 50 percent per year for yearlings and about 80 percent per year for older fish. We are reasonably confident that mean natural mortality of western Lake Erie walleyes older than 1 year has been less than 10 percent per year in recent years. We assume a figure of 10 percent for further discussion.

If we use the simple model of independent mortality factors (Ricker, 1958, Equation 1.7), mean fishing mortality rates are estimated as 44 (limits 33 and 55) percent for yearlings and 78 (limits 67 and 89) percent for older fish. The stated limits assume the 10 percent natural mortality estimate, in the absence of other mortality factors, to be precise.

The “virtual population" estimates for the 1960 to 1963 year classes were about 25,000; 400,000; 2,500,000; and 200,000 fish, respectively. The 1962 estimate of 2.5 million is not much below the previous record year class of 1952 that provided about 3.5 million fish. The latter estimate is obtained from Table 5 of Anon. (1963) in which about 3.0 million walleyes are estimated from data derived from 85 percent of the catch in the period 1953-59. The estimate of 25,000 fish for the 1960 year class is of the same order of magnitude as the 1957 and 1958 year classes; all three are much lower than any other year classes since 1941. We have suggested reasons for such small year classes in a previous section; in a nutshell, we implicate low numbers of spawners, high numbers of predators (small yellow perch, smelt, white bass), and degradation of some spawning areas. That the lake is not yet too eutrophic for the walleye can be inferred from the size of the 1962 year class, its growth rate, and the probable low rate of natural mortality.

Production dynamics

We can investigate the possible effect of different fishing regimes (schedules, quotas, minimum size limits, . . .) on production if we have measures of individual growth rate and mortality rate. We must also consider the possibility that different fishing regimes may affect the various interactions which tend to stabilize the ecosystem.

The mean size of members of different age groups taken by the fishery in the 1962 to 1966 year classes is given in Table 5. For this discussion, we assume that these figures indicate growth rate. We expect true growth rate is overestimated at age I+ and II+, and is underestimated somewhat, thereafter, because of gear selectivity. Our assumptions here, and in what follows, are “conservative” with respect to the conclusions we will draw.

Table 5. Mean weight of walleyes of various ages in samples of commercial landings taken in 1962-1966. Data opposite I, II, ... , apply to mid-spring; those opposite I+, II+, ... , apply to mid-autumn. Assumed mean weight of fish used in models given in extreme right column.

Age	Number of fish	Mean weight (lbs.)	Mean weight used in models (lbs.)
I+	1138	1.14	1.15
II	1427	1.19	1.20
II+	237	1.89	1.90
III	506	2.11	2.10
III+	41	2.81	2.80
IV	103	3.09	3.10
IV+	1	2.30	3.55
V	32	3.80	3.70
v+	3	6.20	4.20
VI	25	4.96	4.60
VI+	1	4.30	5.00
VII	27	6.87	5.40
VII+	0		6.10
VIII	33	8.54	6.50

If the fishery allowed the walleye population to increase (assuming the ecosystem would tolerate an increase), then the growth rate of the walleyes could be expected eventually to decrease due to intraspecific competition. We do not know what the growth rate would be under more moderate fishing pressure. For all of our models we have assumed a more moderate growth rate for V+ and older walleyes than actually observed; these assumed data arelisted in Table 5 (right column).

Following are the details of our models: We assumed a 5 percent natural mortality for each of the half-year periods of mid-spring to mid-autumn, and mid-autumn to mid-spring, for ages beyond II. We have taken fishing and natural mortality as acting in sequence, not simultaneously. This greatly simplifies the calculations and does not introduce serious problems of interpretation, especially since the natural mortality rate is assumed to be so low and the major fishing periods are in fact of relatively short duration. We have further assumed that all fishing occurs at a point in time at mid-spring and another at mid-fall. Again the simplification is not excessive, when compared with reality, in its effect on production estimates.

Table 6 shows the estimates of yield by a year class of walleyes based on the model described above. The initial size of the year class is taken as 3,000,000 yearling (age I) fish in mid-spring. Various fishing mortality schedules are used and the total number of walleyes and their total weight are calculated where all parameters have been maintained exactly as in the model.

The first line in Table 6 provided a sequence of annual catches that resembled closely those of the actual 1962 year class. (The catch curve data suggest that this larger year class suffered a higher fishing mortality than some of the smaller year classes.) Under a fishing intensity that removed 60 percent of extant members each spring and fall, with the harvest beginning in the fall on the yearlings, this year class would yield about 2.76 million walleyes having an aggregate weight of 3.58 million pounds. Over 1,000,000 pounds would be harvested during each of the first 2 years (as yearlings and 2-year-olds). By the third year the catch is about 300,000 pounds, i.e., less than the 500,000 pounds indicated in the table.

The fourth line in Table 6 shows the yield under average fishing conditions in the period 1962-66. The fishing is less intense and the total yield is somewhat more spread out in time. The total yield is about 21 percent higher than that of the first line.

Biologists working on western Lake Erie have recommended repeatedly during the past several years that the fishery allow the fish to become 17 in. (total length) before harvesting and that fishing intensity be limited. Female walleyes currently reach 17 in. at about the end of their third year; at that length and age approximately 50 percent are mature (unpublished U. S. Bureau of Commercial Fisheries data). The last three lines (5, 6, and 7) in Table 6 give estimated yields under such conditions. In these examples, we have shown the fishery commencing with the harvest of 4-year-olds (age-group III) at semi-annual intensities of 70, 50, and 40 percent.

We note that delaying fishing until the walleye reaches age III, even if the intensity be increased somewhat, yields substantially more fish by weight (though smaller numbers). The advantage is increased further if the fishing intensity is decreased further. Thus, we estimate that if fishermen had restricted fishing of the 1962 year class to walleyes of 17 in. long or longer, and had taken only 40 percent of the available fish at each semi-annual interval, they would have landed, in total, about 73 percent more pounds of walleyes than they actually did.

We did not continue the model further because we expect that growth rate would slow somewhat at fishing intensities of less

Table 6. Predictions of yield by a year class of Western Lake Erie walleyes numbering 3,000,000 at age I (mid-spring), natural mortality rate of 5 percent per half-year period, and various fishing mortality schedules.

Text reference ("line")	Six month fishing mortality schedule	Total harvest		Years of harvest of over:	
	Percentage, starting age	Number x 10^6	Weight lbs. x 10^6	1,000,000 lbs.	500,000 lbs.
(1)	60, I+	2.76	3.58	2	2
(2)	50, I+	2.71	3 81	2	2
(3)	30, I+; 50, II	2.70	4.07	2	3
(4)	25, I+; 40, II	2.60	4.34	1	3
(5)	70, III	2.39	5.59	2	2
(6)	50, III	2.32	5.98	2	3
(7)	40, III	2.26	6.18	2	3

than 40 percent each spring and fall. We would, however, expect the relative advantage of diminished fishing to continue to somewhat lower levels of intensity than shown in the last line (7) of Table 6.

We believe that the effects of diminished fishing intensity for walleyes would reverberate throughout the ecosystem. Yellow perch, white bass and perhaps also sheepshead would become somewhat less abundant as a result of predation, would grow more rapidly, and the strength of successive year classes would not fluctuate as violently. We expect, however, that the impact of a considerable reduction in the intensity of the fishery for walleyes would make itself evident primarily among the walleyes themselves and that other species would not be drastically affected by predation.

Regulations and management policies, past and present

The Michigan and Ohio commercial fishery regulations have been enforced rather closely at least since about 1945. One reason for close enforcement was the domination of the fisheries in the Western Basin by trap netters who were politically effective in maintaining regulations that they considered in their best long-term interest. In Ohio, these regulations had been in effect since the early 1930's and included the following: (1) nets could not be set on a reef at any time of year; (2) a closed season was in effect between December 31 and March 15 of each year; and (3) the minimum legal size for walleyes was 13.0 in. (total length). Ohio regulations were conservative with respect to technological innovations. Gill netting was tolerated in the Western Basin, when trap netters were in control, only as long as gill nets remained a minor gear. A second reason for close enforcement was the increasing interest of anglers in the walleye of western Lake Erie, particularly as a result of the high catch rates enjoyed by many during the early 1950's. When walleyes became largely unavailable in the late 1950's, anglers intensified a political campaign to place further restrictions on the commercial fishery which they held partially responsible for the "collapse" of the walleye population. In January 1966, Ohio eliminated the closed season, raised the minimum legal size limit for walleyes to 15.5 in. (total length) and set mesh and area restrictions as follows: (1) Gill net mesh sizes of less than 4-1/4 in. stretched measure were prohibited west of a line extending northward from Huron, Ohio, except between May 10 and June 30; (2) the setting of gill nets of less than 4-1/4 in. stretched measure within one-half mile of shore was prohibited in all Ohio waters east of Huron, Ohio at all times; and

(3) fishermen were restricted from all fishing within one-fourth mile of all legally designated reefs and islands between March 1 and May 9.

Ontario’s Lake Erie fishermen were given gradually increasing freedom to fish as they liked beginning about 1914, and by 1950 the fishery was relatively unregulated. Almost complete freedom existed in 1965, informally if not officially, except that commercial catch statistics had to be submitted on schedule. The fishermen tended to be rather jealous of territorial encroachment from other ports and periodically demanded that the relevant regulations be enforced.

It appears that Ontario’s extreme liberalization of regulations on Lake Erie and lack of interest in enforcing the remaining ones developed from the views of certain advisors and also from the wishes of the larger, technologically advancing, fishery interests along the Ontario shore. The recommendation of one advisor given in 1962 with explicit respect to managing the walleye of western Lake Erie was “to fish the hell out of them.” Though Ontario’s Lake Erie investigators objected immediately to this view, quoting an analysis of production by Regier (1962) similar to that given in Table 6, a laissez-faire attitude became more firmly entrenched judging from subsequent action, or rather lack of action.

In the autumn of 1966, the first step back toward regulation in Ontario’s western Lake Erie waters was taken with a largely unsuccessful attempt to restrict the capture of legally undersized walleyes. This move was followed in the spring 1967 with a trial closed season of a month during the walleye spawning season, to which the fishermen acquiesced since there was little prospect of an economically worthwhile catch at this time.

It may be pertinent here to refer to responses, involving biological principles, that characteristically were made to appeals by concerned fishery biologists that the walleye be granted some protection to permit populations to build up. One type of response was based on views that it was unlikely that a fishery, even if intensive, would act to impair seriously reproductive success and, ultimately, future harvests. Several examples where small “relict” populations had given rise to enormous year classes were referred to as convincing evidence of this view. We have discussed in some detail the concepts from which the above viewpoints derive in previous sections and find them inappropriate to the walleye in the Lake Erie ecosystem. We know of no multi-species fisheries and ecosystems in which they are appropriate.

The literature contains, so far as we know, no closely argued, general attack from a biological viewpoint on a thorough-going laissez-faire attitude towards fish harvesting. That such an approach is likely to be economically inefficient and socially disruptive, even if the ecosystem remains essentially intact, has been adequately demonstrated by Crutchfield and Zellner (1963) and others. Other than for short-run and selfish reasons, we know of no exponents of unregulated, laissez-faire methods (that recognize essentially no property rights) for managing any other organisms (e.g., earthworms, mammals, birds, forest trees, fruit trees, cereals, etc.).

We suggest that the reasons underlying Ontario's recent policy of permitting essentially unregulated fishing in western Lake Erie are an unjustified reliance on high fecundity, a lack of appreciation for the technological sophistication of fishermen, confusion as to the effect of changing environmental conditions (other than man's exploitation), and failure to perceive the role of the fish predator in its ecosystem. If, instead of the first misconception, we substitute "unjustified reliance on a large hatchery program" then these four misconceptions can be blamed for the failure of Michigan and Ohio, particularly Ohio, to maintain essential control over their fisheries about 8 decades ago. We have suggested already that the failure to do so led to the marked fluctuations in herring and blue pike populations at that time. The fact that few "technological improvements" were made in Ohio's fishing methods after about 1930 may be the reason that the fisheries for the various species persisted as long as they did.

In short, it is clear that some government regulation is essential if the walleye fishery of western Lake Erie is ever to recover even a measure of its former importance. On the other hand, we do not expect to see again walleye fishing success of the magnitude that occurred in the middle 1950's. We believe that some of the factors that contributed to those years of plenty have become modified and now act to limit the walleye population, as we have discussed in a preceding section.

Pollution and pollution abatement

Finally, we must consider the practical consequences to the walleye of either intensified pollution or effective pollution abatement in western Lake Erie. Farming practices are becoming increasingly efficient with relatively little loss of phosphates and nitrates to rivers and lakes. This statement now holds in the western Lake Erie drainage area, judging from the work of Harlow (1966). Progress in both water and air pollution abatement is (reportedly) imminent. The Western Basin does not have the essential limnological characteristics of a sewage settling basin. It is flushed by a large volume of relatively infertile water (aside from the pollutants) with a flushing time of about 2 months and would respond to reduced pollution more rapidly than the other lake basins.

The view propagated implicitly and explicitly in the press in recent years by some persons in agencies with responsibilities on the Great Lakes, that once a lake becomes polluted it is “dead,” is simply wrong. We are optimistic about humanity’s ultimate intelligence in reducing pollution, initiating the partial recovery of Lake Erie from its present illness, and returning the walleye to moderate abundance. We find reassurance in the experiences of some European agencies that have attacked the problems that result from enrichment and exploitation with considerably more vigor and success than have their counterparts in North America (see e.g., **Nümann,** 1967).

Similarly, we reject as visionary and unnecessary the suggestion that Lake Erie produce 124 million pounds of fish annually by giving it over to the production of fish protein and by-products. Under such a policy, predators like the walleye, perch, white bass, ... should be eradicated. This latter suggestion obviously collides head-on with the objective of the agencies sponsoring this study, i.e., to find a way of maintaining the walleye stocks.

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