

**MODELING THE WESTERN LAKE  
ERIE WALLEYE POPULATION:  
A FEASIBILITY STUDY**



**Great Lakes Fishery Commission**

**TECHNICAL REPORT No. 32**

The Great Lakes Fishery Commission was established by the Convention on Great Lakes Fisheries, between Canada and the United States, ratified on October 11, 1955. It was organized in April 1956 and assumed its duties as set forth in the Convention on July 1, 1956. The Commission has two major responsibilities: the first, to develop coordinated programs of research in the Great Lakes and, on the basis of the findings, recommend measures which will permit the maximum sustained productivity of stocks of fish of common concern; the second, to formulate and implement a program to eradicate or minimize sea lamprey populations in the Great Lakes. The Commission is also required to publish or authorize the publication of scientific or other information obtained in the performance of its duties.

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# MODELING THE WESTERN LAKE ERIE WALLEYE POPULATION: A FEASIBILITY STUDY

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## FOREWORD

The Great Lakes Fishery Commission is participating in a series of symposia whose subject matter bears on Great Lakes fisheries: Salmonid Communities in Oligotrophic Lakes (SCOL), July 1971; the Percid International Symposium (PERCIS), 24 September-5 October 1976; A Symposium on Selected Coolwater Fishes of North America, 7-9 March 1978; the Sea Lamprey International Symposium (SLIS), scheduled for 1-10 August 1979; and the Stock Concept Symposium, scheduled for 1980.

After concise versions of SCOL papers had been published in the *Journal of the Fisheries Research Board of Canada* (volume 29, number 6, June 1972), it was clear that much detailed information that had been developed by the authors and refined by events at the symposium, and which would be of very considerable value to fishery workers in the Great Lakes area, would not be generally available. The Commission therefore invited the authors of case histories on seven lakes-Superior, Michigan, Huron, Erie, Ontario, Opeongo, and Kootenay-to publish full versions in the Commission's *Technical Report* series (numbers 19-25, 1973).

Similarly, after concise versions of PERCIS papers were published in the *Journal of the Fisheries Research Board of Canada* (volume 34, number 10, October 1977) the Commission asked symposium participants and authors of papers dealing specifically with Great Lakes percids whether more detailed versions of certain papers should be published for the benefit of present and future fishery workers. Based in part on the replies, the Commission authorized publication of *Technical Reports* 31 and 32: "Walleye stocks in the Great Lakes, 1800-1975: fluctuations and possible causes," by J. C. Schneider and J. H. Leach; and "Modeling the western Lake Erie walleye population: a feasibility study," by B. J. Shuter, J. F. Koonce, and H. A. Regier.

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## ABSTRACT

A simple population model of the walleye (*Stizostedion vitreum vitreum*) of western Lake Erie was constructed from a set of empirical relationships linking growth to population density and recruitment to breeding stock size and the spring water temperature regime. Given a reasonable set of values for annual rates of natural and fishing mortalities, consistent with empirical estimates of total survival for the period 1947-75, the model generated a pattern of behavior similar, both qualitatively and quantitatively, to that exhibited by the real population. Two types of stochastic models, based on the initial population model, were used to derive optimal harvest strategies for the population. These strategies were not sensitive to variations in catchability and natural mortality, but the estimated yields produced were highly sensitive to variations in both these factors. A refined and extended version of this model may be useful in developing management policies for this population.

## INTRODUCTION

For well over a century, the western Lake Erie population of the walleye (*Stizostedion vitreum vitreum*) has been subjected to a variety of anthropogenic stresses. These have included a substantial reduction in available spawning areas (Langlois 1945; Regier et al. 1969) and a significant increase in the rate of exploitation (Regier et al. 1969).

Historically, walleyes spawned in many of the western Lake Erie tributaries, in shallow nearshore areas, and on offshore reefs (Langlois 1945; Regier et al. 1969). By the early 1940's, most of the stream spawning areas had been destroyed by dam construction, siltation, pollution, or irregularity of streamflow caused by man's activities (Langlois 1945). By the late 1940's many of the inshore areas had suffered a similar fate (Regier et al. 1969), and only the offshore reefs remained as significant spawning areas (Hartman 1973; Leach and Nepszy 1976). Unfortunately, these mid-lake spawning reefs are vulnerable to a variety of adverse factors such as water currents, turbulence, and temperature reversals. The apparent dependence of the strength of recent year classes on the rate of

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water temperature increase during the spring spawning season can be explained in part by this susceptibility of eggs laid on reefs to destruction by relatively common environmental disturbances (Busch et al. 1975).

Concurrent with, and following, the destruction of the inshore spawning areas, the annual walleye harvest in western Lake Erie varied considerably: the commercial catch remained nearly constant at about 1 million kg per year until the mid-1930's; began to increase slowly, reaching 2.6 million kg in 1950; rose rapidly to an extreme peak of 7 million kg in 1956; and then fell precipitously to less than 0.5 million kg in 1961. It remained low until 1969, when the commercial fishery was closed because of mercury contamination. The rapid increase in production, beginning in the early 1950's, was accompanied by a significant increase in the rate of exploitation. It has been suggested (Regier et al. 1969) that standardized fishing effort for walleyes in Canadian waters was perhaps 50 times greater in the late 1950's than in the late 1940's.

These variations in the commercial catch were accompanied by several significant changes in the walleye population and the fishery: a progressive decline in catch per unit effort (Table 1); a sharp decline in year-class strength (Parsons 1970; Regier et al. 1969); a truncation of the age

Table 1, Summary of data on annual trap-net catch of walleyes per unit effort (kg/lift) for all statistical districts in western Lake Erie. Data in italics are from Regier et al. (1969) and the others are from Kutkuhn et al. (1976).

Year	Statistical district <sup>a</sup>						
	Mich.	O-1		O-2	OE-1		OE-2
1948	-	<i>15.9</i>		-	-		5.4
1949		19.8		-	-		5.0
1950	-	20.3		-	8.8		6.2
1951	27.1	20.0		-	12.6		6.5
1952	33.8	16.0		-	17.3		5.7
1953	48.5	23.5		-	14.7		5.1
1954	32.0	20.7		-	19.0		6.0
1955	47.3	30.5		-	29.0		5.7
1956	51.8	30.8		-	18.6	22.9	6.6
1957	56.5	23.6		—	12.1	12.3	4.2
1958	42.7	18.7		—	8.5	8.4	1.7
1959	18.8	7.2		-	2.9	2.9	0.95
1960	14.5	8.3	8.4	2.6	2.7	2.7	0.59
<b>1961</b>	10.7	1.9	5.3	3.3	2.7	2.7	0.50
<b>1962</b>	8.0		3.7	2.9		1.5	0.68
<b>1963</b>	16.5		8.0	4.5		2.2	0.77
1964	20.9		5.6	3.2		1.2	0.59
<b>1965</b>	12.9		4.4	2.3		3.1	0.86
1966	12.9		3.5	2.5		2.9	1.0
<b>1967</b>	42.2		5.6	4.0		6.3	1.0
<b>1968</b>	19.2		17.6	4.4		1.8	-
<b>1969</b>	13.1		9.0	2.5		2.3	-

a See Smith et al. (1961) for detailed boundaries of districts. Districts O-1 and O-2 include Ohio waters west of Fairport, and districts OE-1 and OE-2 include Ontario waters west of the boundary of Elgin and Kent counties.

distribution (Busch et al. 1975; Parsons 1970); and a progressive increase in length at age (Parsons 1970). In the years after the ban on commercial fishing, most of these trends have reversed.

As noted by Regier et al. (1969), this set of events conforms closely to the typical pattern expected during the "fishing-up" period (Ricker 1975) which generally follows a significant increase in exploitation rate. The recent authors who have reviewed the history of this population (Busch et al. 1975; Hartman 1973; Nepszy 1977; Regier et al. 1969) seem to be in general agreement that the rate of exploitation reached nonsustainable levels in the mid-1950's and that this was a primary, if not the major, factor responsible for some or all of the changes listed above.

Combining this interpretation of events with the known dependence of year-class strength on the spring warming rate leads to a rather simple qualitative model of the population consisting of two major elements: a standard, hump-shaped stock-recruitment relation, modified by the influence of the spring warming rate; and a negative relation between growth rate and population size, offset by a positive relation between growth rate and forage density. In this paper, we attempt to carry out three objectives: (1) evaluate the data base for the population to determine if sufficient information exists for the derivation of quantitative estimates of these basic relations; (2) incorporate the estimated relations into a quantitative dynamic model of the population and determine if its behavior is consistent with observed behavior; and (3) explore some of the ways in which such a quantitative model could be used in managing the population. The supporting data and the methodology are given in much greater detail than in the earlier summary by Shuter and Koonce (1977).

## DATA BASE: SOURCES AND PRELIMINARY MANIPULATIONS

The character and origins of the data base are summarized in Table 2. The relations of interest have stock abundance, or the abundance of some part of the stock, as the independent variable or the dependent variable, or both. Therefore, it was essential to develop closely comparable indices of stock abundance for as many years as possible.

### Abundance indices

Following other authors (Kutkuhn et al. 1976; Parsons 1970; Regier et al. 1969), we assumed that data from commercial trap-net catches in United States waters provided the most reliable available information on long-term changes in the population. Concurrent information on the catch per unit effort (CPE) in kilograms per lift, age distribution, and mean weight per fish was available for both fall and spring catches in Michigan and statistical district O-1 (Smith et al. 1961) of western Ohio (Tables 3 and 4). Unfortunately, the spring series was short (1962-69) and the fall series

Table 2. Types and sources of primary data sets relating to the western Lake Erie walleye.

Information	Period	Source
Catch and effort data by gear, statistical district, year, and season	1939-69 <sup>a</sup>	Regier et al. (1967, 1969), Kutkuhn et al. (1976)
Age compositions of commercial catches by gear, statistical district, year, and season	1943-70 <sup>a</sup>	Busch et al. (1975), Parsons (1970), Kutkuhn et al. (1976)
Mean weights of fish in fall trap-net catches	1943-62	Parsons (1970)
Catch indices for young-of- the-year	1959-75	Kutkuhn et al. (1976)
Lengths at various ages	1920-67 <sup>a</sup>	Adamstone (1922) Deason (1933), Lawler (1948) Parsons (1970, 1972), Wolfert (1977)
Weights at various ages	1962-66	Regier et al. (1969), Kutkuhn et al. (1976)
Lengths and ages at maturity	1927-66 <sup>a</sup>	Deason (1933), Wolfert (1969)
Spring water temperatures	1918-74 <sup>a</sup>	Anonymous (1961), Ohio Department of Natural Resources (unpublished data)

<sup>a</sup> Data lacking for some years in period.

was incomplete in both districts. The following manipulations were carried out to extend and complete the fall CPE series for 1948-69 in Ohio and 1946-69 in Michigan.

In Ohio for 1960-69, the total fall catch was taken almost entirely with trap nets (Kutkuhn et al. 1976) and the fall trap-net effort was highly correlated ( $r = 0.87$ ,  $n = 10$ ) with the total trap-net effort for the year. Assuming these relations to hold for 1948-59, we derived estimates (Table 3) of the fall CPE for this period from the annual trap-net effort and fall trap-net catch data given by Kutkuhn et al. (1976) and Regier et al. (1967, 1969).

Estimates (Table 3) of the fall CPE in Michigan for 1946-50 were derived as follows: the total fall catch was multiplied by the fraction of the annual catch taken in trap nets to estimate the fall trap-net catch (data from Regier et al. 1967); and the fall effort was assumed to have remained constant at 662 lifts, the mean fall effort for 1951-59.

To derive concurrent indices of relative abundance for different age groups (i.e., number of walleyes caught per trap-net lift) from the CPE data, we also needed to know the mean weight and the age distribution of fish in the catch for each year. Such detailed information was available for all of the spring catches in Michigan and western Ohio (Table 4) and for the fall catches for 1943-69 in Ohio and 1963-69 in Michigan (Table 3). Regression analysis showed the Michigan observations to be closely similar, both qualitatively and quantitatively, to those made in Ohio over the

Table 3. Summary of fall data on trap-net catch of walleyes per unit effort (CPE; kg/lift), mean fish weight (kg), and age composition (%) in western Ohio (district 0-1) and Michigan waters of Lake Erie. Mean weights in Ohio for 1946-62 are from Parsons (1970).

Mean weights for 1963-69 were calculated from the age distributions and the fall weight-at-age schedule given by Regier et al. (1969). Italicized CPE values are estimates (see text for explanation).

Year	Source													
	Ohio							Michigan						
	CPE (kg)	Mean wt (kg)	Age (years)					CPE (kg)	Mean wt (kg)	Age (years)				
1			3	3	4	≥5	1			2	3	4	≥5	
1946	-	0.44	1.6	41.9	38.0	15.5	3.2	29.1	—	-	-	-	-	-
1947	-	0.48	1.0	11.6	58.1	19.2	10.1	25.9	—	-	-	-	-	-
1948	13.4	0.48	5.5	58.6	18.6	8.6	8.7	24.2	—	-	-	-	-	-
1949	12.4	0.45	5.1	40.5	38.6	9.5	6.3	23.6	—	-	-	-	-	-
1950	14.4	0.34	10.0	56.7	23.3	9.3	0.7	43.5	—	-	-	-	-	-
1951	9.8	0.44	2.0	40.6	46.5	6.9	4.0	18.4	-	-	-	-	-	-
1952	10.5	0.44	7.5	47.1	33.3	9.2	2.9	25.2	-	—	-	-	-	-
1953	9.6	0.42	1s.o	51.1	21.8	10.5	1.6	16.8	-	—	-	-	-	-
1954	14.4	0.45	5.1	73.0	18.2	3.6	0	24.7	-	—	—	-	-	-
1955	9.4	0.65	21.1	29.1	36.0	11.4	1.7	14.0	-	—	—	-	-	-
1956	14.9	0.56	18.5	69.6	40.0	4.6	3.3	22.0	-	—	—	-	-	-
1957	9.3	0.62	40.3	32.9	20.8	5.4	0.6	26.6	-	—	—	—	—	—
1958	4.5	0.84	29.0	54.1	11.3	2.4	3.2	8.5	-	—	—	—	—	—
1959	0.79	1.00	40.0	27.2	20.0	5.5	7.3	4.9	-	—	—	—	—	—
1960	8.3	0.50	97.0	2.1	0.5	0.4	0	16.6	-	—	—	—	—	—
1961	1.3	0.85	14.4	79.7	5.2	0.7	0	6.7	-	—	—	—	—	—
1962	0.97	0.86	67.8	9.7	19.3	0	3.2	5.0	-	—	-	-	-	-
1963	8.4	0.53	99.0	0.7	0	0.3	0	18.5	0.52	99.3	0.7	0	0	0
1964	1.8	0.65	63.9	33.8	2.3	0	0	5.5	0.68	49.5	45.7	1.7	0	0
1965	1.4	0.61	83.9	8.2	6.7	0.3	0.9	3.7	0.68	72.3	13.9	12.3	0	1.5
1966	0.82	0.53	92.2	5.7	2.1	0	0	9.0	0.54	94.1	5.9	0	0	0
1967	4.7	0.87	1.6	96.8	0.3	1.3	0	8.0	0.87	3.0	94.7	0.7	1.3	0
1968	0.97	0.81	53.4	14.6	32.0	0	0	4.0	0.79	56.8	15.1	28.1	0	0
1969	1.2	0.71	58.2	34.3	2.9	4.6	0	3.3	0.68	67.2	24.8	4.0	4.0	0

Table 4. Summary of spring data on trap-net catch of walleyes per unit effort (CPE; kg/lift), mean fish weight (kg), and age composition (%) in western Ohio (district O-1) and Michigan waters of Lake Erie. Mean weights in both districts were calculated from the age distributions and the spring weight-at-age schedules given by Kutkuhn et al. (1976) and Regier et al. (1969).

Year	Ohio					Michigan				
	CPE (kg/lift)	Mean wt (kg)	Age (years)			CPE (kg/lift)	Mean wt (kg)	Age (years)		
			1	2	≥3			1	2	≥3
1951	-	-	-	-	—	33.9	-	-	-	-
1952	-	—	-	-	—	38.4	-	-	-	-
1953	-	—	-	-	—	72.0	-	-	-	-
1954	-	—	-	-	—	41.5	-	-	-	-
1955	-	-	-	-	—	75.5	-	-	-	-
1956	-	—	-	-	—	74.4	-	-	-	-
1957	-	—	-	-	—	83.3	-	-	-	-
1958	-	—	-	-	—	59.1	-	-	-	-
1959	-	—	-	-	—	24.6	-	-	-	-
1960	9.7	—	-	-	—	13.0	-	-	-	-
<b>1961</b>	7.2	-	-	-	-	13.2	-	-	-	—
<b>1962</b>	5.3	1.64	0	4.0	96.0	9.2	1.07	0	13.1	<b>86.9</b>
<b>1963</b>	<b>6.5</b>	0.77	0	78.4	21.6	12.0	-	—	—	-
1964	<b>8.6</b>	0.58	0	92.8	7.2	26.6	0.67	0	<b>89.1</b>	10.9
<b>1965</b>	<b>7.4</b>	0.87	0	46.6	53.4	16.7	0.98	0	14.0	86.0
1966	5.0	0.91	0	63.0	37.0	14.1	0.68	0	78.7	21.3
<b>1967</b>	<b>5.4</b>	0.79	0	55.7	44.3	54.9	0.66	0	82.0	18.0
1968	<b>26.6</b>	0.98	0	1.4	98.6	28.9	1.04	0	<b>1.0</b>	99.0
<b>1969</b>	<b>12.5</b>	1.25	0	16.7	83.3	16.5	0.58	0	<b>58.0</b>	42.0

same period. Therefore we concluded that, where necessary, data on mean weights and age distributions collected in Ohio could be used with CPE data from both Ohio and Michigan in deriving indices of stock abundance. This adjustment enabled us to derive separate sets of abundance indices for age groups I through IV, and for all age groups combined, from the Ohio data for 1948-69 and the Michigan data for 1946-69.

### Annual survival rates

Separate estimates of the annual survival rate for each of the age groups II, III, and IV were derived from the Ohio and Michigan abundance indices for 1947-69. We then averaged concurrent estimates; omitted obviously anomalous values (those for 3-year-olds in 1964 and for 4-year-olds in 1957 and 1967); and smoothed variations over time, using 3-year running averages, to give the values required (Fig. 1). An upper limit of 80% was imposed to conform with an annual natural mortality of 20% (Kutkuhn et al. 1976)--a somewhat higher value than that given by Regier et al. (1967, 1969). These results were interpreted as follows.

In the years before 1958 and after 1965, 1-year-old fish were not fully recruited into the fall trap-net fishery (Busch et al. 1975; Parsons 1970). Therefore, the abundance indices for 1-year-olds are negatively biased in these years, leading to anomalously high estimates of survival rates for 2-year-olds. Similarly, the rapid decrease in the estimated survival rate for 3-year-olds, in the period immediately before 1954, suggests a similar bias in the abundance indices for 2-year-olds in the years before 1953.

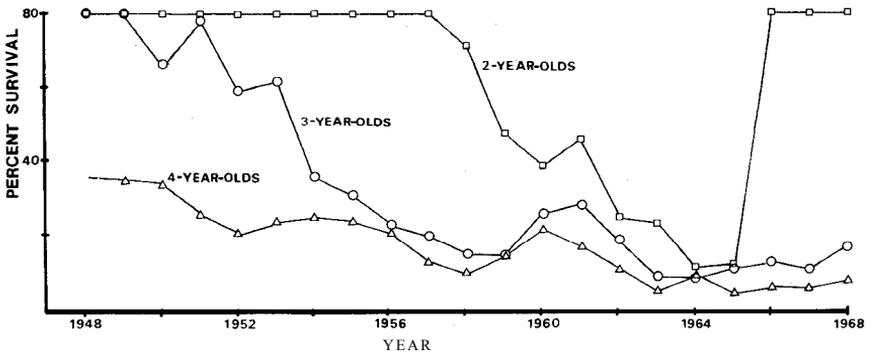


Figure 1. Annual survival rates for age groups II, III, and IV, obtained by averaging independent estimates from Michigan and Ohio abundance data and smoothing the curves by using 3-year running averages.

In the years when the index for 1-year-olds was biased but the index for 2-year-olds of the same year class was not, we derived corrected indices as follows:

$$\text{Corrected } I_1^i = I_2^{i+1} / \left[ \frac{\phi_2^{i+1} + \phi_3^{i+1}}{2} \right] \quad 1$$

where  $I_j^i$  is the observed fall abundance for age  $j$  fish in year  $i$  and  $\phi_j^i$  is the estimated survival rate for age  $j$  fish in year  $i$ , as given in Fig. 1. For the years in which the indices for both the 1- and 2-year-olds for the same year class were biased, but the index for 3-year-olds was not, we determined corrected indices as follows:

$$\text{Corrected } I_1^i = \left[ I_3^{i+2} / \left( \frac{\phi_3^{i+2} + \phi_4^{i+2}}{2} \right) \right] / \left( \frac{\phi_2^{i+1} + \phi_3^{i+1}}{2} \right) \quad 1$$

By applying these procedures to the indices derived from Michigan data, we developed a complete set of corrected abundance indices (Table 5) for various segments of the stock over the period 1946-68.

### Spring water temperature data

Busch et al. (1975) noted that, from 1960 to 1970, recruitment was strongly dependent on the rate of water temperature increase over the spawning reefs from 6 April to 15 May, an interval which consistently included the major walleye spawning period. To investigate this effect further, we used water temperature data collected near the spawning reefs at South Bass Island (Ohio) to calculate the rate of water temperature increase over this interval for each year from 1918 to 1974 (Table 6). Inspection of graphs of water temperature vs. time suggested that the rate of temperature increase for this period was not representative, in some years, of the average rate prevailing during the spawning period (determined from the observation by Wolfert et al. 1975 that walleye spawning in western Lake Erie peaks at 7° C). We adjusted the calculation interval to correct for this discrepancy.

Considering all estimates from 1918 to 1974, the distribution of the spring rate of water temperature increase was approximately normal, with a mean of 0.215 Celsius degrees per day and a standard deviation of 0.069.

Table 5. Corrected abundance indices (number of walleyes caught per trap-net lift) for walleyes of various ages, derived from fall catch data collected in Michigan.

Year	Age (years)			
	1	≥2	≥3	≥4
1946	22.1	90.0	36.3	112.1
1947	43.7	66.8	49.8	110.5
1948	54.8	53.8	18.8	108.6
1949	50.3	72.1	28.3	122.4
1950	59.8	68.7	31.8	128.5
1951	28.8	71.3	23.9	100.1
1952	28.8	46.3	25.9	75.1
1953	69.0	34.1	13.6	103.1
1954	11.2	52.1	11.9	63.3
1955	52.5	16.9	10.6	69.4
1956	28.2	32.1	4.65	60.3
1957	12.5	25.5	11.4	38.0
1958	4.2	7.2	1.7	11.4
1959	2.0	3.0	1.62	5.0
1960	32.2	1.0	0.3	33.2
1961	1.1	6.74	0.46	7.84
1962	4.0	1.90	1.3	5.9
1963	34.8	0.35	0.11	35.15
1964	5.4	3.1	0.19	8.5
1965	5.1	0.98	0.47	6.08
1966	19.1	1.32	0.36	20.42
1967	1.6	9.1	0.15	10.7
1968	2.35	2.3	1.58	4.65
1969	-	1.92	0.35	-

## STOCK-RECRUITMENT RELATION

To investigate the form of the stock recruitment relation, we used the abundance indices given in Table 5 to derive annual indices of breeding stock size and year-class strength for 1947-67.

The first step in deriving a measure of size of the breeding stock was to define the age of maturity. Data on age of maturity for western Lake Erie walleyes were presented by Deason (1933) for fish caught in 1927-28, and by Wolfert (1969) for fish caught in 1964-66. Both authors found a strong relation between total length and the percentage of mature fish. However, the total length at which maturity among females exceeded 8% was 35 cm in 1927-28 (Deason 1933) and about 45 cm in 1964-66 (Wolfert 1969). In both studies, males were found to mature at a shorter length than females. Concurrent with this change in length at maturity was a significant increase in length at age (Table 7). Assuming that these two events were related and occurred in concert (Hile 1954; Wolfert 1969), it follows, from Parsons' (1970) data on length at age, that: (1) Deason's findings should be approximately valid at least until 1947;

Table 6. Estimated rates of spring water temperature increase, obtained from linear regressions on temperature vs. date, for the time intervals shown.

Year	Starting date in April	Ending date in May	Slope (C°/day)
1947	6	15	0.18
1948	6	15	0.19
1949	6	2	0.21
1950	6	15	0.22
1951	6	15	0.23
1952	6	15	0.27
1953	1	15	0.18
1954	6	15	0.21
1955	6	15	0.29
1956	6	15	0.20
1957	1	31	0.21
1958	6	15	0.17
1959	6	15	0.24
1960	12	15	0.18
<b>1961</b>	3	15	0.24
<b>1962</b>	8	15	0.29
<b>1963</b>	5	15	0.20
1964	1	15	0.32
<b>1965</b>	1	15	0.36
1966	<b>1</b>	15	0.10
<b>1967</b>	<b>8</b>	15	0.13
1968	8	15	0.12
<b>1969</b>	7	15	0.24
1970	7	15	0.31
1971	1	18	0.21
1972	6	15	0.20
1973	1	15	0.17
1974	6	15	0.19

Table 7. Total length (cm) and age at maturity of walleyes (males and females combined) in western Lake Erie from 1927 to the mid-1960's.

Year	Length at age III	Length at age IV	Maximum length at which less than 20% were mature	Minimum length at which 80% or more were mature	Source
1927-28	28.5	34.5	30.8	33.7	Deason (1933)
1947	32.0	38.6	-	-	Lawler (1948)
1954	34.8	37.3	-	-	Parsons (1970)
1957	38.1	44.2	-	-	Parsons (1970)
1960	43.7	48.0	-	-	Parsons (1970)
<b>1963-67</b>	45.0	51.3	41.2	43.3	Wolfert ( <b>1969</b> , 1977)

Lawler's (1948) data on length at age then imply that in 1947 40% of the 3-year-old, and all of the 4-year-old and older, fish were mature; and (2) Deason's length-maturity relation indicates that most fish aged 3 and over were mature from 1954 on, and Wolfert's length-maturity relation indicates that most fish aged 3 and over were mature from 1960 on. In the absence of information on the exact manner in which length at maturity changed over the critical period from 1947 to 1960, we made the following assumptions in deriving indices of abundance for mature fish: (1) in 1946-69, all fish 4 years old and older were mature; (2) in 1946-47, 40% of the 3-year-olds were mature; (3) in 1954-67, 100% of the 3-year-olds were mature; and (4) from 1948 to 1953, the percentage of mature 3-year-olds increased linearly.

Regression analyses (Table 8) indicated that fall abundance indices could be used to derive two independent indices of the spring abundance of potential spawners: (1) an index based on the abundance of fish 2 years old and older in the fall of the year preceding the year of spawning; and (2) an index based on the abundance of fish 3 years old and older in the fall of the year of spawning. Given this result and the above assumptions regarding age at maturity, we developed indices of breeding stock size for each of the years from 1947 to 1967, using the abundance indices given in Table 5.

In recent years, estimates of the fall density of young-of-the-year walleyes (based on index catches in experimental trawls) have served as useful measures of recruitment to the fishery by individual year classes, thus indicating that year-class strength is generally set by the end of the first growing season. Unfortunately, values for this index are available only for 1959-75; however, fall abundance indices for 1-year-olds are available for 1946-69 (Table 5). Use of these figures as consistent indicators of recruitment to the population at age I in 1946-68 is valid only if at least one of the following conditions holds: (1) the total mortality rate, from hatching to the end of the 2nd year of life, shows no long-term trend over the period 1946-68; (2) trends in mortality, from hatching to the end of the 2nd year of life, are not reflected in the CPE values used. There is

Table 8. Results of regression analyses of the relation between indices of the spring abundance of mature fish, derived from trap-net catch data collected in the spring, and similar indices derived from data collected in the fall. The symbol  $I_k^i$  represents the CPE of fish aged  $k$  years and over, in year  $i$ . The period covered by each variable is also given.

Nature of regression (M = Michigan, 0 = Ohio; (F) = fall, (S) = spring)	Period	Correlation coefficient	No. of points
$\bar{I}_3^i M(S)$ vs. $\bar{I}_3^i M(F)$	1962-69	0.91	7
$\bar{I}_3^i M(S)$ vs. $\bar{I}^{i-1} M(F)$	1961-68	0.89	7
$\bar{I}_3^i O(S)$ vs. $\bar{I}_3^i O(F)$	1962-69	0.83	8
$\bar{I}_3^i O(S)$ vs. $\bar{I}^{i-1} O(F)$	1961-68	0.95	8

no direct evidence of a long-term trend in the natural mortality rate of young fish. Fishing pressure on young-of-the-year walleyes has always been negligible or lacking (Busch et al. 1975; Parsons 1970; Regier et al. 1969). However, fishing pressure on 1-year-olds increased significantly because of the introduction and widespread use of gillnets of small and intermediate mesh size, primarily in Canadian waters, and because of the increase in growth rate, which made yearlings increasingly vulnerable to the fall trap-net fishery (Busch et al. 1975; Parsons 1970; Regier et al. 1969). For these changes in the fishing mortality rate of 1-year-olds to be strongly reflected in the fall CPE data from Michigan, extensive movement of 1-year-olds from Canadian to Michigan waters during the spring and summer of each year would be required. The tagging studies of Ferguson and Derksen (1971) and Wolfert (1963) showed, however, that such movement of yearlings did not occur. Therefore, we concluded that the known trends in the overall mortality rate for young fish in this population were probably not strongly reflected in the fall abundance indices for 1-year-olds derived from Michigan catches, and that these figures could serve as a consistent index of recruitment to the population at age I in 1946-68. The high correlation of this index with both the index catches for young-of-the-year ( $r = 0.89$  for year-classes 1959 to 1967), and Parsons' (1970) virtual population estimates of year-class strength ( $r = 0.863$  for year classes 1945 to 1961), provides empirical support for these conclusions.

After converting the recruitment and stock size indices to logarithms, we performed step-wise multiple regression analyses to estimate the relation linking recruitment to breeding stock size and the spring rate of water temperature increase for the year classes from 1947 to 1967. A separate analysis was carried out for each of the two indices of breeding stock size available. Both analyses produced similar results (Table 9): a strong dependence of recruitment on both the size of the breeding stock and the spring rate of increase in water temperature. In the relation between recruitment and stock size, the slope decreases monotonically with increasing stock size, indicating that the left half of a typical, hump-shaped

Table 9. Results of multiple regression analyses of the relation linking recruitment (R) to breeding stock size (S) and the rate of water temperature increase in the spring ( $\Delta T$ ), in which stock size indices were based on the fall abundance of fish 3 years old and older ( $I_{3+}$ ) and 2 years old and older ( $I_{2+}$ )

Multiple	Fitted parameters ( $\pm$ SD in parentheses):			
		$\log R = \alpha + \beta \log S + \delta \Delta T$		
r	$\alpha$	$\beta$	$\delta$	
$I_{3+}$ 0.837	0.009 (0.28)	<b>0.488</b> <b>(0.09)</b>	<b>4.016</b> <b>(1.23)</b>	
$I_{2+}$ 0.804	-0.42 (0.32)	0.53 (0.11)	4.422 (1.35)	

stock-recruitment curve is involved. The temperature effect is multiplicative and independent of stock size, and thus in accord with Kicker's (1975) general analysis of the probable effects of physical environmental factors on recruitment.

To derive a single relation linking the number of yearlings in the spring of one year to the breeding stock size and spring water temperature regime of the preceding year, we made the following modifications to the results in Table 9:

(1) Estimated values for each of the coefficients in the two analyses were weighted according to the inverse of their variances and averaged to obtain:

$$\text{Recruitment} = 0.663 \left[ \begin{array}{c} \text{Breeding} \\ \text{stock} \\ \text{index} \end{array} \right] 0.505 \left[ \begin{array}{c} \\ \\ 15850 \end{array} \right] \Delta T \quad (1)$$

where  $\Delta T$  is the spring rate of water temperature increase in Celsius degrees per day and both of the abundance indices are in Michigan CPE units.

(2) Since equation (1) was derived in part by regressing the logarithm of the recruitment index on the untransformed rate of water temperature increase, the resulting equation predicts the geometric mean of the recruitment index (Ricker 1975); we obtained an expression that predicts the arithmetic mean by multiplying the right-hand side (RHS) of (1) by 1.366.

(3) The recruitment index was assumed to be roughly proportional to the total number of yearlings in the fall if natural mortality alone had been operating on the population; to adjust for the effects of natural mortality on yearlings from spring to fall, we divided the RHS of (1) by the half-year survival rate corresponding to an annual survival rate of 80% (Kutkuhn et al. 1976).

(4) Kutkuhn et al. (1976) estimated that, for 1963-69, the average number of western Lake Erie walleyes 1.5 years old or older was about 1.5 million, and the average fall CPE in Michigan for this same period was about 13.0; thus absolute numbers of fish can be estimated by multiplying CPE values by 115,400. This conversion factor was substituted into (1) to convert it from relative to absolute units. After applying the above modifications 2, 3, and 4 to equation (1), we arrived at the equation:

$$R = 325 S^{0.505} (15850)\Delta T \quad (2)$$

where,  $R$  is the number of yearlings in spring of year  $i$ ,  $S$  is the number of mature fish in spring of year  $i - 1$ , and  $\Delta T$  is the rate of water temperature increase (Celsius degrees per day) in the spring of year  $i - 1$ .

Before developing the remaining relations required by our population model, we treat certain aspects of the multiple regression analyses in

more detail. There are similar secular trends in the data for both stock size and recruitment. Therefore the strong correlation between these two variables may not stem from a causal connection, but rather from the action of some additional factor(s), such as fishing or increased natural mortality, operating to reduce both stock size and recruitment over about the same period. This possibility cannot be definitively rejected on the basis of the available data. However, the following results provide additional support for the causal interpretation.

After converting to logarithms, we fitted third-degree polynomials to the data on both recruitment and stock size to remove the secular trends. We then repeated the multiple regression analyses, using the deviations of recruitment and stock size from the fitted trend lines (Table 10). Removal of the secular trend greatly reduced variation in stock size and correspondingly diminished the apparent strength of the stock effect. However, in both analyses a positive stock effect was still detectable and the fitted values for both the stock and temperature coefficients were roughly comparable with those obtained from the analyses of the raw stock and recruitment data.

Using a different approach, we divided the data set into two subgroups of equal size: an earlier group for the year classes from 1947 to 1956 and a later group for the year classes from 1958 to 1967. Separate log-log regressions of recruitment on stock size were calculated within each group (Table 11). In each pair of subgroups, the means for the stock size were separated by at least an order of magnitude; nevertheless, a positive effect of stock on recruitment was detectable in both groups, and the slope estimates were roughly similar in value to each other and to the corresponding slope estimates of Table 9.

All of these results offer support for the view that a relatively stable relation, linking recruitment at age I to stock size and the spring water temperature regime, was operative in this population over the period 1947-67.

Table 10. Results of multiple regression analyses of the relation linking recruitment (R) to breeding stock size (S) and the rate of water temperature increase in the spring (AT), in which stock size indices were based on the fall abundance of fish 3 years old and older ( $I_{3+}$ ) and 2 years old and older ( $I_{2+}$ ). Stock and recruitment data were adjusted to eliminate secular trends.

Multiple r	Fitted parameters ( $\pm$ SD in parentheses): $\log R = a + \beta \log S + \delta AT$		
	a	$\beta$	$\delta$
$I_{3+}$ 0.731	-0.9471 (0.26)	0.3198 (0.27)	4.343 (1.16)
$I_{2+}$ 0.728	-1.031 (0.27)	0.2726 (0.25)	4.729 (1.10)

Table 11. Results of log-log regressions of recruitment (R) on breeding stock size (S), based on subsets of the 1947-67 data set.

Basis of stock index	Log S		Correlation coefficient <sup>a</sup>	Slope
	Mean	Range		
Catch of fish 3 years old and older				
1947-56	1.180	0.667 to 1.480	0.623	0.743
1958-67	-0.358	-0.958 to 0.230	0.439	0.557
Catch of fish 2 years old and older				
1947-56	1.657	1.227 to 1.801	0.486	0.775
1958-67	0.400	-0.453 to 1.406	0.248	0.251

a None of the correlation coefficients are statistically significant.

## RELATIONS BETWEEN GROWTH RATE AND POPULATION DENSITY

Implicit in the qualitative model outlined in the preceding section is the assumption that the observed trend in growth rate was caused by a gradual reduction in intraspecific competition for food. Detailed elaboration of such a relation would require concurrent information on densities of both forage and walleye populations. Since extensive information on forage density was not available, we restricted our analysis to an attempt to relate growth rate to population density.

When the total length after four growing seasons for each year class from 1947 to 1963 (Parsons 1970; Wolfert 1977) was plotted against the abundance index of fish 1 year old and older for the year when the year class was hatched (Fig. 2), the relation between these two quantities was adequately described by the equation

$$L_4 = 51.6 - 0.673 e^{0.027I_{1+}}$$

where  $L_4$  is the total length (cm) after four growing seasons and  $I_{1+}$  is the abundance index for fish 1 year old and older in the year when the year class was hatched. This relation was derived from a log-log regression of  $(L_4 - 51.6)$  on  $Z_{1+}$ . Conversion of the equation to absolute units on the basis of the abundance index conversion factor given in the preceding section yields

$$L_4 = 51.6 - 0.673 e^{(0.23 \times 10^{-6})} (\text{no. fish aged } 1+) \quad (3)$$

Since this relation can be used to predict the average length of fish in a year class after four growing seasons, all that is now required is a means of predicting the length at other ages from the length at age IV. Data on

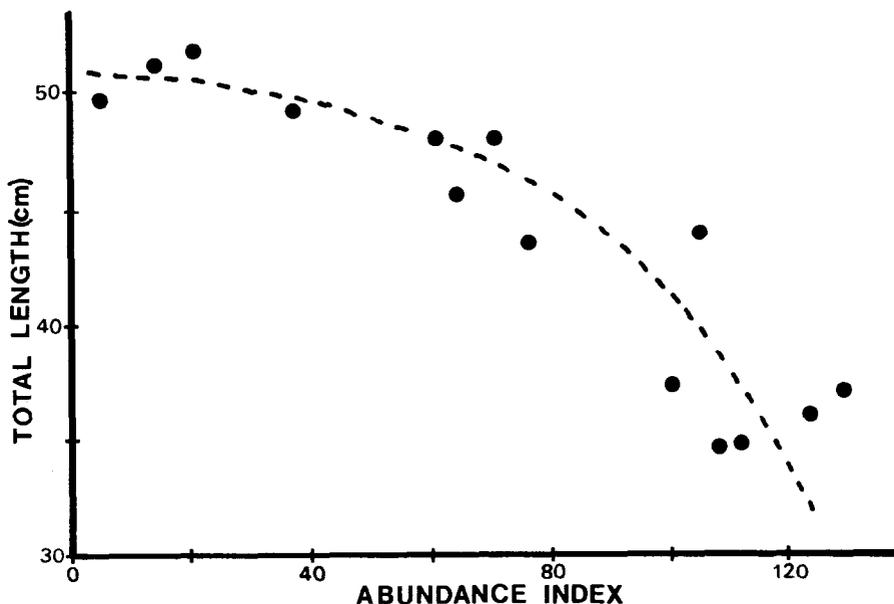


Figure 2. Relation between total length after four growing seasons, for year classes from 1947 to 1963, and the abundance index (number of fish per trap-net lift) for fish 1 year old and older in the year when the year class was hatched.

the total lengths at various ages given by Adamstone (1922), Deason (1933), Lawler (1948), Parsons (1972), and Wolfert (1977), plotted in Fig. 3, conform rather closely to the equation

$$L_{t+1} = 12.4 + .836 L_t \quad (4)$$

where  $L_t$  is total length (cm) at age  $t$  and  $L_{t+1}$  is total length 1 year later. This relation, or its inverse, can then be used in conjunction with equation (3) to predict variations in length at any age from variations in population density. Variations in weight can be predicted from variations in length by using the length-weight relation for western Lake Erie walleyes published by Baker et al. (1976)

$$W = 1.32 \times 10^{-2} L^{2.9302} \quad (5)$$

where  $W$  is weight in grams and  $L$  is total length in centimeters.

## STRUCTURE AND BEHAVIOR OF THE POPULATION MODEL

The relations (2) through (5), given in preceding sections, form the heart of the model population. Age groups I through VIII are represented

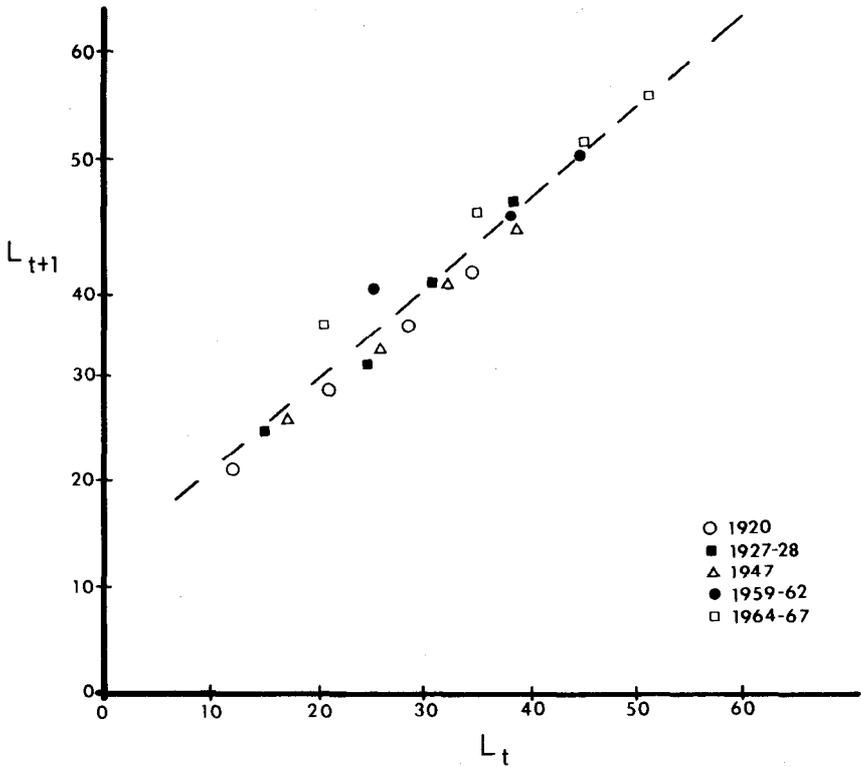


Figure 3. Walford plot of total length-at-age data (length in centimeters) collected in various years over the period 1920-67.

explicitly, with a constant annual natural mortality rate of 20% (Kutkuhn et al. 1976) imposed on each group. A minimum length at age I, equivalent to the minimum observed length during 1927-66 (15.2 cm; Deason 1933), is also imposed on the model. Known changes in the age at maturity are accounted for in the manner outlined earlier. The total fishing mortality for each year is assumed to occur at one time, in the middle of the growing season. A listing of the FORTRAN program for the model is given in Appendix A.

The behavior of the model was compared with that of the real population for 1947 to 1975. Initial population size in the spring of 1947 was estimated from the fall abundance indices for 1946 and 1947. Three annual survival rate schedules, A through C, were used. In all three, the survival rates of fish 4 years old and over for 1947 through 1969 were taken from the estimates for 4-year-olds given in Fig. 1 (values for 1947 and 1969 were assumed to be equal to those for 1948 and 1968, respectively). Values for 1970 to 1975 were taken from Kutkuhn et al. (1976). Recognizing the known positive bias in the survival estimates for 2- and 3-year-olds in some years, we assumed that the actual survival rates for each of the age

groups from I through III were bounded above by the estimates given for the group in Fig. 1, and below by the estimates for fish 4 years old and older. An upper bound of 80%, corresponding to the action of natural mortality alone, was assigned to the survival rates for 1-year-olds. In general the values in schedule A were chosen from the upper regions of their respective ranges and the corresponding values in schedule B from the lower regions. A detailed description of the derivation of the survival rates in each schedule is given in Table 12.

The simulated catches produced by schedules A and B bracket the observed catches (Fig. 4). Under A, the simulated catch peaks later than the observed catch and then declines to an average level considerably higher than that observed. Under B, the simulated catch peaks earlier and at a lower level, and then declines to an average level only slightly higher than that observed. These results suggest that, until the mid-1950's, the schedule B survival rates are somewhat lower than those experienced by the real population, whereas from the mid-1950's to the end of the 1960's, the schedule A survival rates are somewhat higher.

Schedule C (Fig. 5) was constructed with this interpretation in mind. From 1947 to 1953, survival rates similar to those in schedule A are used. From 1954 to 1956, there is a transition to a set of rates similar to those in B, which then continue in effect until 1975. These trends in survival are consistent with the following sequence of events: In the early 1950's, an increase in the use of small- and large-mesh gillnets, a decrease in the minimum size limit in Canadian waters, and a steady increase in growth rate led to a rapid increase in fishing mortality, particularly among the younger fish (Busch et al. 1975; Regier et al. 1969). Beginning in 1966, however, increases in minimum size limits (Busch et al. 1975) and their enforcement (Regier et al. 1969) led to a reduction in fishing mortality among these younger fish. This age-dependent differential in fishing mor-

Table 12. Derivation of survival rate schedules A and B for 1948-68 and 1970-75. Rates in 1947 and 1969 are assumed to be equal to those in 1948 and 1968, respectively.  $A_j^i$  and  $B_j^i$  represent the survival rates of age  $j$  fish in year  $i$  for schedules A and B;  $\phi_j^i$  represents the survival rate of age  $j$  fish in year  $i$  as given in Fig. 1;  $K^i$  represents the average survival rate in year  $i$  given by Kutkuhn et al. (1976).

Age group	Schedule A		Schedule B	
	Period	Derivation	Period	Derivation
IV-VIII	1948-68	$\sim i = \phi_4^i$	1947-75	$B_j^i = A_j^i$
	1970-75	$A_j^i = K^i$		
III	1948-53	$A_{3j}^i = (\phi_3^i + \phi_4^i)/2$	1947-75	$B_{3j}^i = A_{3j}^i$
	1954-68	$A_{3j}^i = \phi_3^i$		
	1970-75	$A_{3j}^i = K^i$		
II	1948-58	$A_{2j}^i = (\phi_2^i + \phi_3^i)/2$	1947-65	$B_{2j}^i = A_{3j}^i$
	1959-65	$A_{2j}^i = \phi_2^i$	1966-75	$B_{2j}^i = A_{2j}^i$
	1966-68; 1970-75	$A_{2j}^i = (A_{3j}^i + 0.8)/2$		
I	1948-68; 1970-75	$A_{1j}^i = (A_{2j}^i + 0.8)/2$	1945-65	$B_{1j}^i = A_{2j}^i$
			1966-75	$B_{1j}^i = A_{1j}^i$

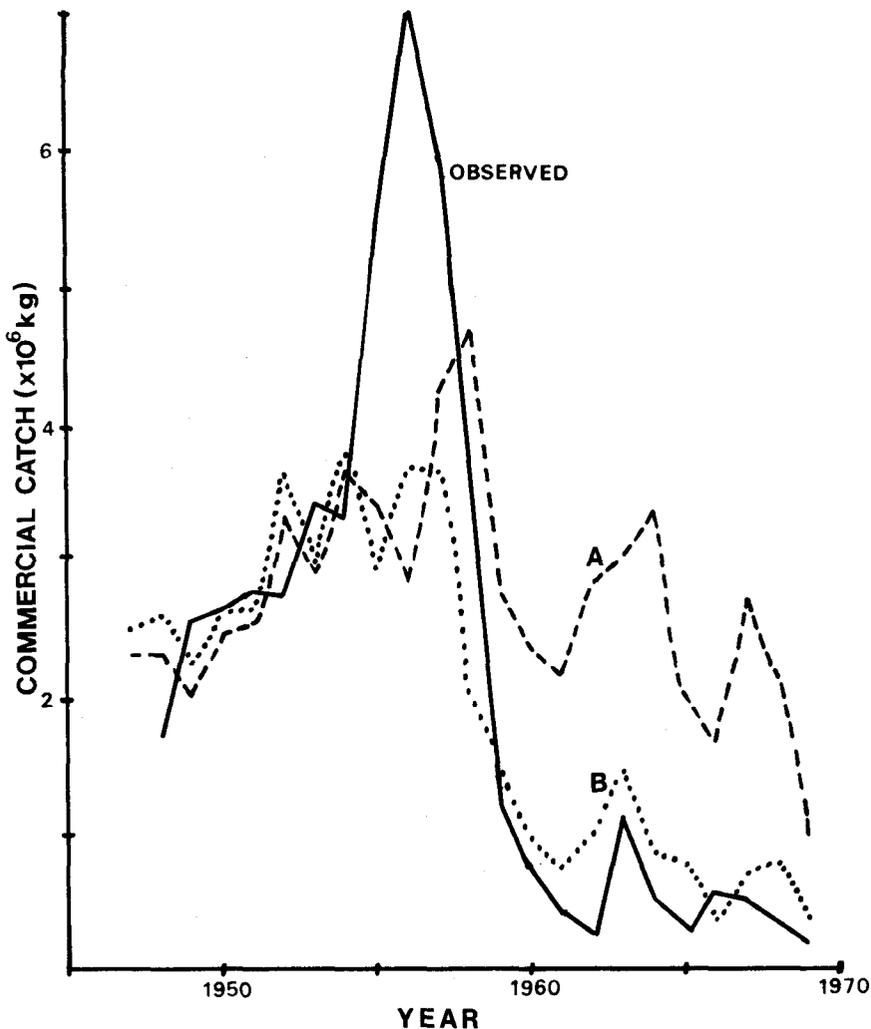


Figure 4. A comparison of observed catches in the commercial fishery with catches generated by the model based on survival rate schedules A and B. (See text for derivation of the schedules.)

tality was maintained during the 1970's, when only a sport fishery was active (Baker et al. 1976; Duckworth and Paine 1975).

In general, the behavior of the model under schedule C (Figs. 6-10) is similar to that shown by the real population. In particular, the observed increase in recruitment after 1968 is predicted reasonably well, as is the increase in overall abundance—the predicted 1975 abundance levels corresponding roughly to Nepszy's (1977) evaluation of the current status of the population. Only the simulated lengths at various ages (Fig. 10) differ

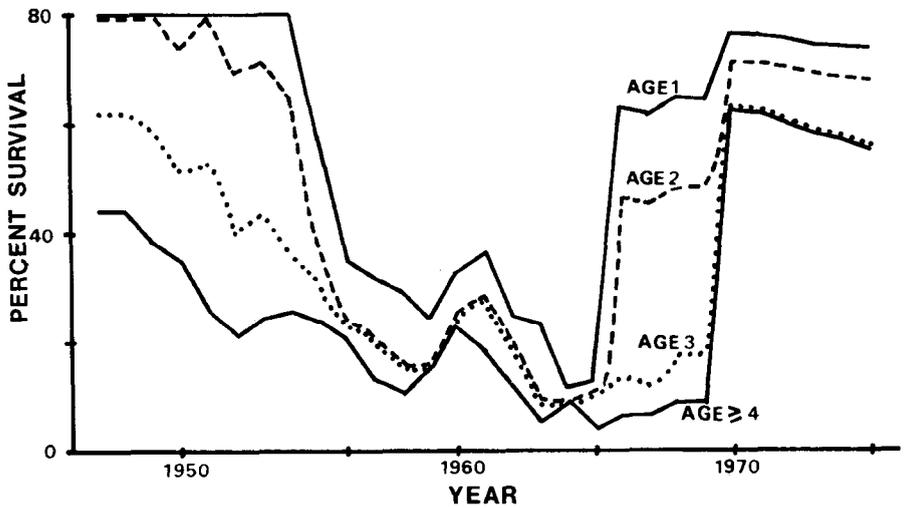


Figure 5. Annual survival rates, by age groups, used in schedule C. (See text for derivation of the values.)

consistently from those observed. If the observed values for length at age IV are imposed on the model rather than the values generated by equation (3), the simulated commercial catch follows a pattern almost identical with that observed (Fig. 6).

## EVALUATION OF ANALYSES AND SIMULATION STUDIES

We have shown that the available information on relative abundance, year-class strength, and growth for western Lake Erie walleyes can be used to construct a quantitative version of the qualitative model outlined in the introductory sections. We have also shown that a reasonable representation of the actual fishing mortality regime in 1947-75 elicits from this model a general pattern of behavior closely similar to that shown by the real population. Furthermore, both the extent and rapidity of the recovery in year-class strength and general abundance after 1968 are predicted with reasonable accuracy. Since the data used to derive the basic relations for the model extended only to 1968, the continued correspondence between real and predicted behavior beyond this date suggests that quantitatively similar relations were still operative in the population and that the model has true predictive capabilities.

Although the level of agreement between simulated and observed behavior is reasonably high, it is not perfect. Perhaps the most significant discrepancy is in the strength of the 1955 year class: the model predicted that it was very strong, whereas the observational index suggested that it was only of moderate strength. This discrepancy is important because the height of the peak in the simulated commercial catch is determined in part

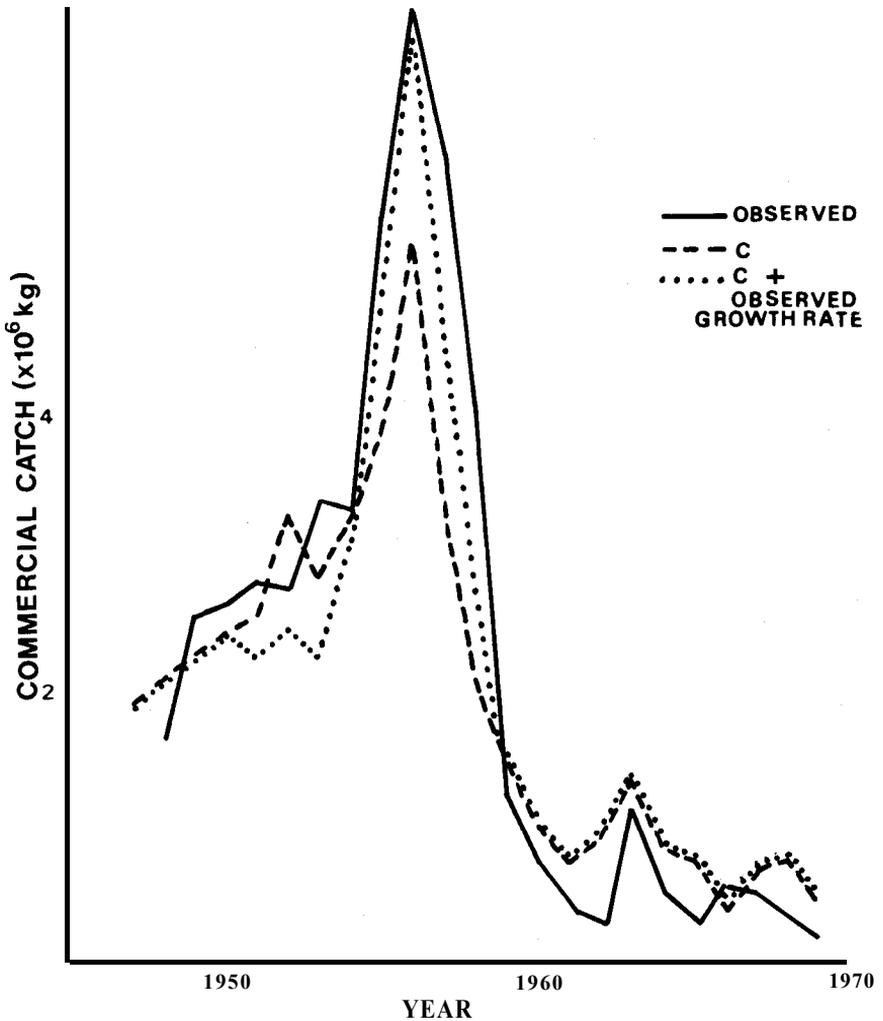


Figure 6. A comparison of the observed catches in the commercial fishery with catches predicted by the model, based on survival rate schedule C alone and survival rate schedule C plus observed growth rate.

by the strength of the 1955 year class. However, it is difficult to assess the true extent of this disagreement. The fact that catches in small-mesh gillnets were highest over the period 1956-58 (Kutkuhn et al. 1976; Regier et al. 1969), the same period when the 1955 year class would have been most susceptible to this type of gear, suggests that this year class may actually have been strong.

The ability of the model to reproduce historical changes in relative abundance does not stem solely from the fact that data on these same changes were used in deriving the model. The fit to historical data was

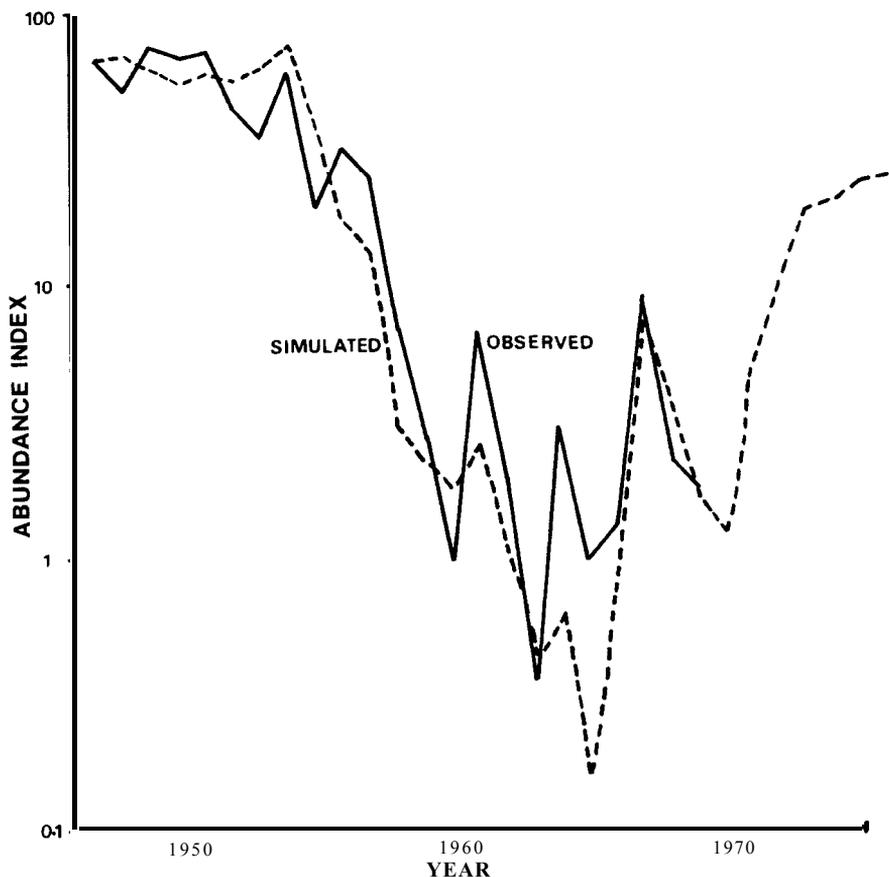


Figure 7. A comparison of the observed abundance indices (number of fish per trap-net lift) for fish 2 years old and older with values generated by the model based on survival rate schedule C.

obtained by comparing observed and simulated commercial catches. The generation of these values required that independent information on the following three factors be incorporated into the model: natural mortality, the relation between absolute population size and the relative abundance index used, and the relation between length and weight. It does not follow that such a model would necessarily be capable of generating reasonable commercial catch values for 1947 to 1969 simply because it was derived in part from estimates of relative abundance and lengths at various ages for this same period. Similarly, even if reasonable catch values could be generated under a realistic fishing mortality regime, it does not follow that the corresponding behavior of other population indices would necessarily mimic their observed behavior. This behavior of the model suggests that the various measures of abundance, year-class strength, and growth used

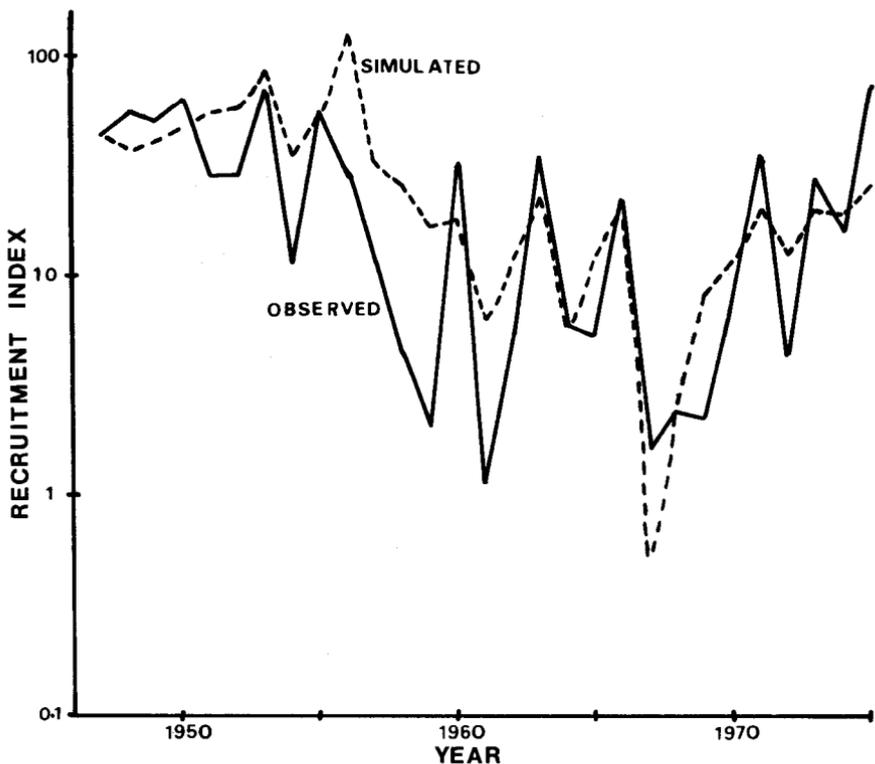


Figure 8. A comparison of the observed values for the recruitment index (number of 1-year-olds per trap-net lift) with values generated by the model based on survival rate schedule C.

in deriving it were reasonably consistent and representative, and that, given the levels of recruitment observed, the loss to the fishery over this time period was sufficient to account for the observed decline in overall abundance.

## ANALYSIS OF ALTERNATIVE HARVEST STRATEGIES

We attempt now to derive an optimal harvest strategy for the population, allowing for the known effects of climatic variations on recruitment, and to evaluate the sensitivity of such a strategy to changes in growth rate, gear selectivity, and natural mortality.

### Cohort yield model

Much theoretical work has focused on determining the maximum yield obtainable from a single cohort of a multi-age fish stock. Beverton

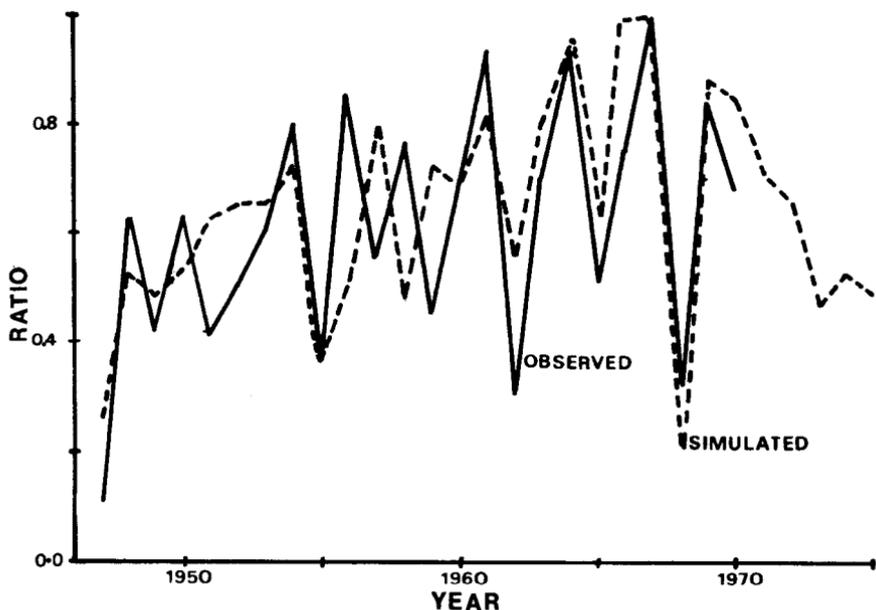


Figure 9. A comparison of observed values, for the ratio of the abundance of 2-year-olds to the abundance of fish 2 years old and older, with values generated by the model based on survival rate schedule C.

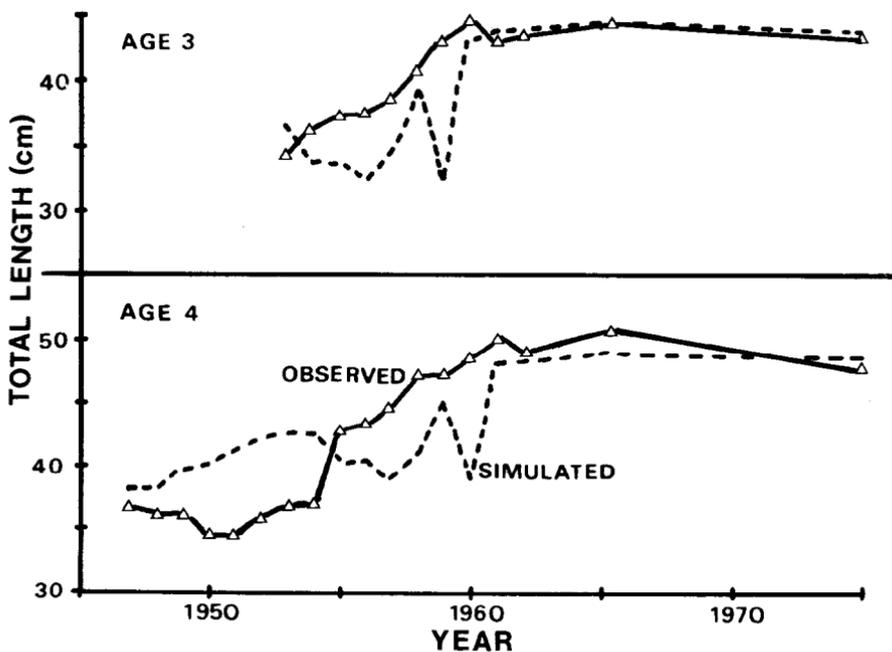


Figure 10. A comparison of observed lengths (solid line) at ages 3 and 4 with lengths generated by the model based on survival rate schedule C (broken line).

and Holt (1957) showed that yield curves peak at low fishing mortality rates when the natural mortality is low. At high natural mortality rates these peaks disappear, and maximum yields are then obtained at high fishing mortality rates. Thus, a strategy to maximize yield from a cohort will be sensitive to estimates of natural mortality.

We used the following model to assess the effects of variations in natural mortality and catchability on maximum cohort yield:

$$N_{i+1} = N_i e^{-(F_i + M_i)}, i = 1 \text{ to } 10$$

$$F_i = fq_i$$

$$Y = \sum_{i=1}^{10} W_i \frac{F_i}{F_i + M_i} (N_i - N_{i+1})$$

where  $N_i$  is the number of fish aged  $i$  at the start of the year,  $F_i$  and  $M_i$  are the instantaneous rates of fishing and natural mortality for age  $i$  fish,  $f$  is the fishing effort,  $q_i$  is the catchability of age  $i$  fish,  $Y$  is the total yield from the cohort, and  $W_i$  is the weight of age  $i$  fish halfway through the growing season. Values for  $W_i$  were calculated from equations (4) and (5), assuming a length at age I of 15.2 cm. A value of 5 million fish was assumed for  $N_1$ .

The optimal fishing effort generated by this model varied for different age-dependent catchability regimes and for different natural mortality rates. To illustrate the first effect, we used two extreme catchability regimes, reflecting early and late entry into the fishery (regimes I and III, Table 13). The late-entry regime approximates the real situation for western Lake Erie walleyes in 1948, and the early-entry regime the real situation in 1963. In both, the catchability coefficients for fish of age IV and older were set equal to 1.0, reflecting full recruitment to the fishery. A third catchability regime (II, Table 13), intermediate between I and III, was used to illustrate the effects of variations in the natural mortality rate on the optimal fishing effort.

Optimal efforts and yields were higher for the delayed-entry regime than for the early-entry regime (Table 13, Fig. 11); also increasing effort beyond the optimum did not decrease yield as rapidly in the delayed-entry situation as it did in the early-entry one. Increasing the natural mortality rate leads to an increase in the optimal effort and a decrease in the yield produced by that effort.

#### Stochastic population yield model

An analysis of the maximum yield derivable from individual cohorts is of limited use in determining strategies to maximize sustainable yield. An

Table 13. Maximum annual yields and optimal fishing efforts for a single cohort and for a population under various entry and natural mortality regimes. Catchability values for age I through III are defined as follows: regime I--0.17,0.47,0.83; regime II--0.05,0.50, 1.0; and regime III--0.0,0.02,0.42. A value of 1.0 is assigned to fish 4 years old and older. Natural mortality coefficients are the same for all age classes.

Entry regime	Natural mortality coefficient	Cohort <sup>a</sup>		Population	
		optimal effort (yr <sup>-1</sup> )	Maximum yield (10 <sup>6</sup> kg/yr)	optimal effort (yr <sup>-1</sup> )	Maximum yield (10 <sup>6</sup> kg/yr)
I	0.2	0.4	2.1	0.2	5.3
III	0.2	0.7	2.5	0.3	6.8
II	0.203	0.406	2.116	0.202	5.426
II	0.4	1.0	1.3	0.5	1.5

<sup>a</sup>Initial density:  $5 \times 10^6$  1-year-olds, each with a total length of 15.2 cm.

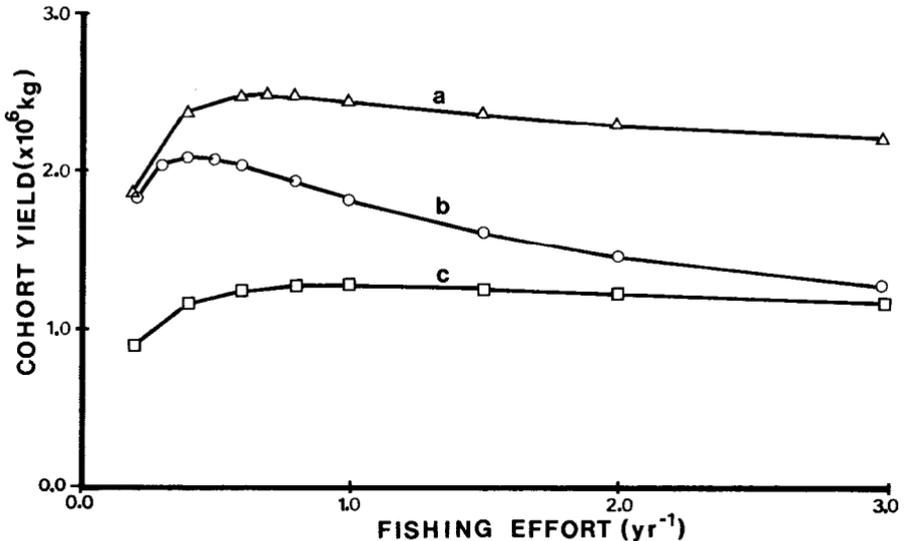


Figure 11. Curves of yield vs. effort for a single cohort. The three curves represent different natural mortality rates ( $M_i$ ) or entry regimes (see Table 13): a—entry regime I,  $M_i = 0.2$ ; b—entry regime III,  $M_i = 0.2$ ; and c—entry regime II,  $M_i = 0.4$ . Initial conditions:  $5 \times 10^6$  yearlings with a total length of 15.2 cm.

equally important factor is future recruitment through natural reproduction. Using the stock-recruitment relation derived for this population, we extended the previous analysis of yield to include the effects of breeding stock size and climatic variation. The model for this analysis is functionally identical with that used to describe the historical behavior of the population. However, instead of using observed rates of spring warming, we simulated the catch for a hundred-year period, using a sequence of

warming rates drawn at random from the empirically determined probability distribution for that quantity.

The effects of variations in natural mortality and catchability on optimal effort are not as strong in these population simulations as they are in the cohort simulations (Table 13). However, the effects on the maximum yield are somewhat stronger, and the yield curves for the population are more sharply peaked than those for the cohort (Fig. 12). Delayed entry into the fishery again produced a higher yield, which showed less response to increasing effort. However, the predictions of high yields at low efforts may be suspect.

A major deficiency in the population model is the assumed constancy of natural mortality. At low fishing mortalities, the relatively low estimate for natural mortality (20%) causes the total instantaneous mortality rate to be low. Under these conditions, the population density increases to high levels because the slope of the stock-recruitment relation decreases slowly to zero with increasing stock size, and therefore does not act to stabilize population density. Although our analysis of the data on breeding stock size and recruitment did not reveal a dome-shaped stock-recruitment curve, general considerations as well as evidence from other populations (e.g., Forney 1976) suggest that some form of density-dependent regulation should occur. It is not known, however, whether

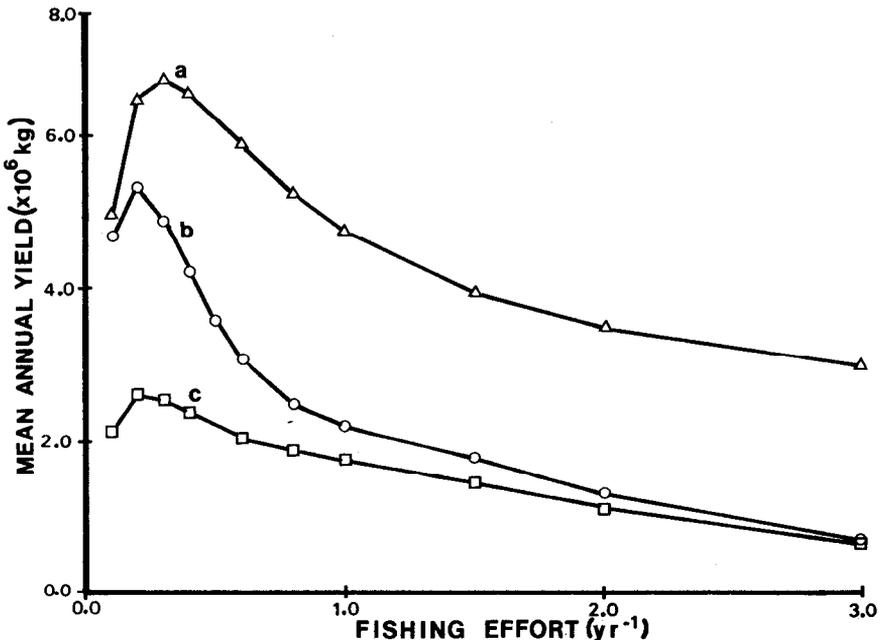


Figure 12. Mean annual yields from a walleye population subjected to constant fishing effort for a hundred-year period. The three curves reflect different natural mortality rates ( $M_i$ ) or entry regimes (see Table 13): a—entry regime I,  $M_i = 0.2$ ; b—entry regime III,  $M_i = 0.2$ ; and c—entry regime II,  $M_i = 0.3$ .

this regulation will be reflected in the natural mortality rates of yearling and older fish or in the mortality of eggs, larvae, and juveniles. Without this information, one cannot place much confidence in the high mean annual yields predicted for relatively low levels of fishing effort. A greater degree of reliability can be attached to the general pattern of response exhibited by the optimal fishing effort to the kinds of changes in the character of the fishery explored in these simulation studies.

### Stochastic dynamic programming analysis

Another approach for estimating the maximum sustainable yield of walleyes in western Lake Erie is to determine the balance between yield and future recruitment from the cohort. A technique to evaluate optimal fishing effort in this way can be derived from the principles of stochastic dynamic programming (Walters 1975). This technique allows the development of management strategies based on standing stock, or some other measure of population density, and a particular management objective (e.g., maximum sustainable yield or minimum variation in catch). The dynamic programming approach applied to fisheries by Walters (1975) was designed for populations with nonoverlapping generations. Since walleyes do not conform to this assumption, we used a modified version of Walters' approach.

Instead of focusing on the total stock, we determined the optimal effort for exploiting a cohort throughout the time it is in the population. This was done by assigning to each cohort, of a given size at age I, a numerical value equal to the total yield derived from that cohort plus the mean annual value of the offspring of that cohort. The degree of fishing effort that maximized this value was defined as the optimal effort. The value of the offspring was determined from their number by a recursion process described by Walters (1975). The number of offspring was a function of the number of reproducing adults in the cohort and the rate of spring warming. A stochastic element was introduced into this scheme by defining the spring warming rate in terms of its empirically determined probability distribution. The model which forms an essential part of this analysis was based on the cohort yield model described above and the stock-recruitment relation. A listing of the FORTRAN program for this model is given in Appendix B. Index catch values for young-of-the-year were used as indicators of numerical abundance at age I. Recruitment to the fishery was defined by the moderate-entry regime described earlier (regime II, Table 13). A constant annual natural mortality rate was assumed for all age groups.

This approach yielded an optimal control law for the fishery defined in terms of the optimum harvest appropriate to a year class whose strength was characterized by a particular value for young-of-the-year (Fig. 13). The range of fishing effort required to implement this law over the range of such index values considered was given in terms of a frequency distribution (Fig. 14).

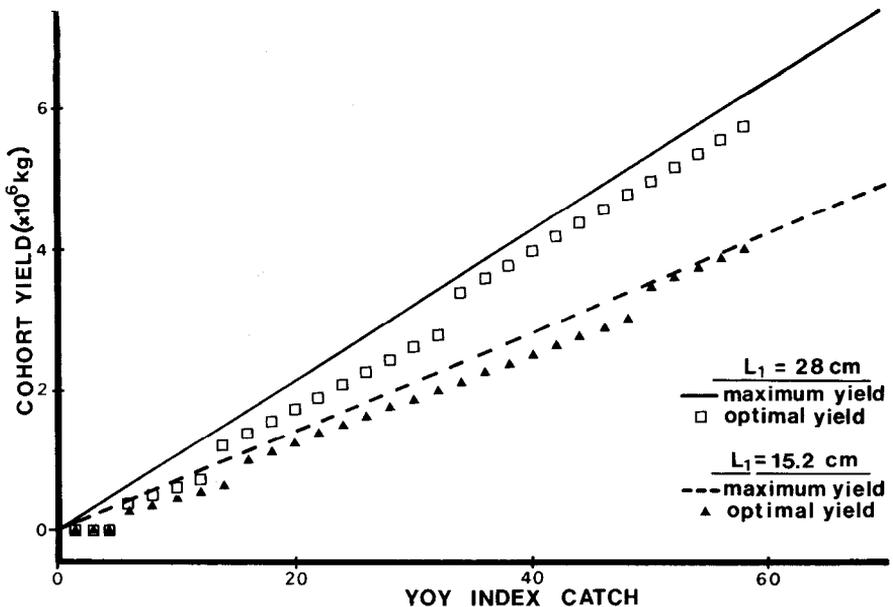


Figure 13. The relation between optimal cohort yield and cohort strength, generated by the dynamic programming technique, for two growth rates ( $L_1 = 15.2$  cm, and  $L_1 = 28$  cm). The corresponding relations between maximum cohort yield and cohort strength are also included.

Our analysis of the growth rates of individual walleyes revealed a density-dependent effect. Although this regulation of growth is included explicitly in the long-term population model described earlier, its effects could only be explored indirectly by using the dynamic programming approach. We did this by carrying out separate analyses, assuming that: (1) the young-of-the-year index represents recruitment to a population with low overall density, thus allowing a high rate of growth for recruits ( $L_1 = 28$  cm); or (2) the index represents recruitment to a dense population, thus imposing a low growth rate on recruits ( $L_1 = 15.2$  cm). The instantaneous natural mortality rate was held constant at 0.2. As expected, a higher growth rate resulted in higher yields (Fig. 13) and slightly higher effort (Fig. 14a, b). In both situations, the optimal cohort yields calculated by this approach were not much lower than the maximum yields obtainable when no value was attached to future recruitment from the cohort (Fig. 13). Despite the differences in yield due to differences in growth rate, predictions of optimal effort were similar to those generated by the long-term population model. The optimal control laws in Fig. 13 indicate an optimal fishing effort of 0.2 per year with highest frequency (Fig. 14a). This prediction corresponds well with the prediction of the population model (Table 13). Furthermore, increasing the natural mortality rate to 0.4 per year leads to an optimal effort prediction of 0.5 to 0.6 (Fig. 14c), which again corresponds with the predictions of the population model (Table 13).

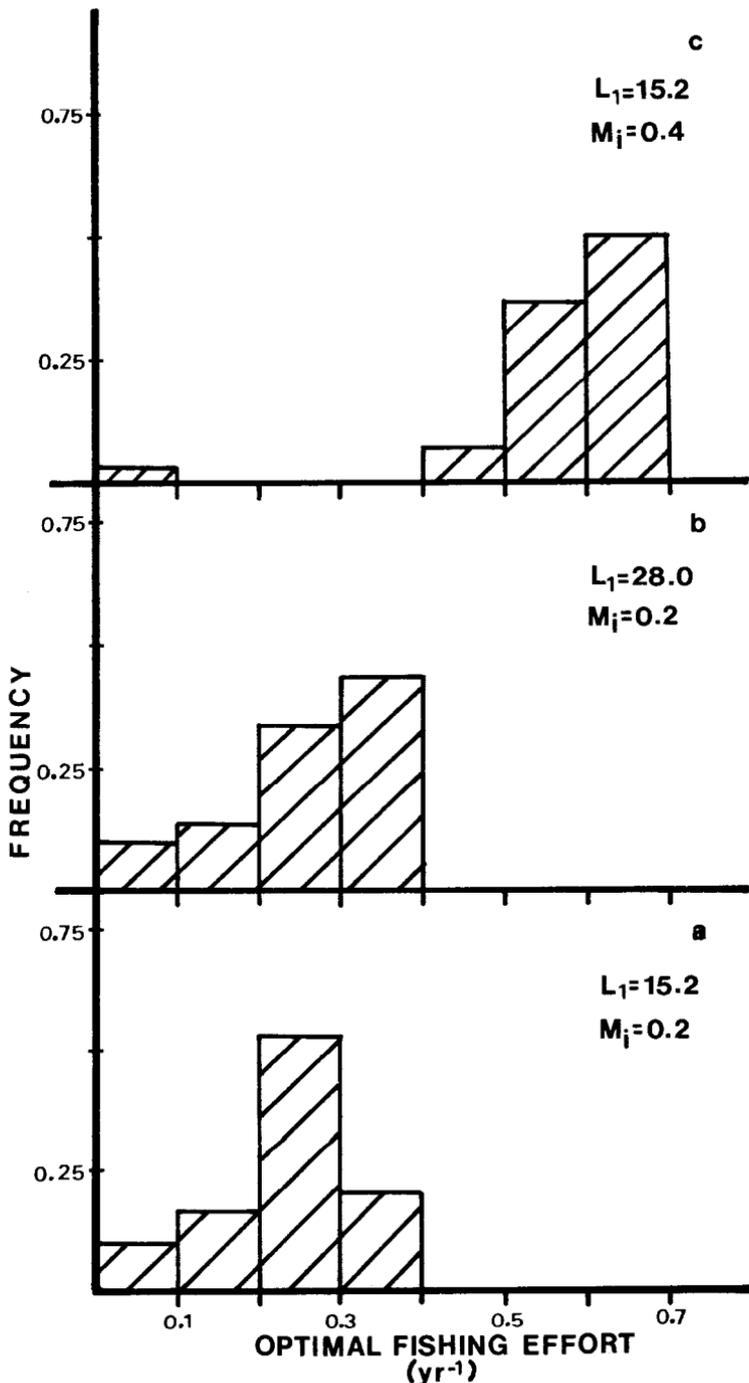


Figure 14. Frequency histograms for the optimal fishing efforts associated with the optimal cohort yields given in Figure 13 (lower and center panels, a and b) and for a condition of increased natural mortality (upper panel, c).

## EVALUATION OF OPTIMAL HARVEST STRATEGIES

The similarity of the predictions of optimal effort generated by the two models that consider both yield and future recruitment suggests that a more efficient management policy could be developed for the exploitation of walleyes in western Lake Erie. However, the magnitude of the resulting catches is beyond existing predictive capability. The optimal catches generated by these models probably overestimate the optimal catches actually obtainable. This overestimation is due in part to our inability to define the effects of high population densities on the mortality rates operative at various life stages. For the same reason, it is not certain that the actual yield vs. effort curve would exhibit the sharp peak at low fishing efforts which was characteristic of the curves generated by our models. A broad dome in this curve would allow a fairly wide range of fishing effort without major differences in yield.

Nevertheless, both models indicate optimal instantaneous fishing mortality rates of 0.2 to 0.3 per year, assuming a value of 0.2 for the natural mortality rate. Even at higher natural mortality rates, the optimal fishing mortality rate does not increase beyond 0.6 per year. These figures are in sharp contrast to those obtained from the estimated survival rates in Fig. 1. Assuming a natural mortality rate of 0.2, the fishing mortality rates for fully recruited age groups range from 0.7 in 1948 to 2.8 in the mid-1960's-values that indicate that this population has long been exploited at levels beyond the optimum.

The simulation results also demonstrate that a catchability regime that emphasizes delayed entry into the fishery yields greater harvests, which are less sensitive to supra-optimal exploitation, than does a regime which allows early entry.

## CONCLUSIONS

Analysis of the data made available to us suggests that greatly increased exploitation of western Lake Erie walleyes during the 1950's and 1960's reduced population abundance to very low levels over a relatively short time. Data collected during this period appear to contain extractable information on the relations linking year-class strength to breeding stock size and the spring water temperature regime, as well as on the relation linking growth rate to population density. A model based on preliminary estimates of these relations was relatively successful in accounting for the known behavior of the population and was readily adaptable for use as a management tool. It may be possible to extend and refine this model sufficiently for use in developing realistic management policies for the population.

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APPENDIX A

C \*\*\*\*\*WESTERN LAKE ERIE WALLEYE POPULATION MODEL\*\*\*\*\*

C THE BASIC PROGRAM INCLUDES THE FOLLOWING ASSUMPTIONS:

- C (1) THE POPULATION IS MADE UP OF AGE GROUPS 1 THROUGH 8 (YOUNG OF YEAR  
C IGNORED)
- C (2) ALL FISH AGED THREE AND OVER ARE FULLY MATURE
- C (3) THE EMPIRICAL RELATIONSHIPS LINKING GROWTH & A RELATIVE MEASURE OF  
C THE ABUNDANCE OF RECRUITS TO MEASURES OF RELATIVE POPULATION ABUNDANCE  
C (CPE) ARE USED EXPLICITLY; THESE RELATIVE MEASURES OF ABUNDANCE ARE  
C CONVERTED TO ABSOLUTE NO'S USING INPUT (RNPCE,RNPYGY) VARIABLES
- C (4) ALL MORTALITY OCCURS HALF-WAY THROUGH THE GROWING SEASON OF EACH YEAR
- C (5) THE NATURAL MORTALITY RATES FOR ALL AGE GROUPS ARE EQUAL (=RNM,  
C AN INPUT VARIABLE) AND DO NOT VARY FROM YEAR TO YEAR
- C (6) THE ANNUAL SURVIVAL RATES FOR FISH AGED 4 AND OVER ARE EQUAL

C THE PROGRAM ALLOWS FOR:

- C (1) INPUT OF TWO SETS OF ANNUAL SURVIVAL RATES FOR EACH AGE GROUP  
C (ARRAY SURV) AND THE CAPACITY TO SHIFT FROM THE FIRST TO THE SECOND AT  
C ANY PARTICULAR YEAR (INPUT VAR. IYRSW)
- C (2) ANNUAL VARIATIONS IN THE PERCENT OF 3 YEAR-OLDS WHICH ARE MATURE  
C (ARRAY CORMAT)
- C (3) INTRODUCING ANNUAL DEVIATIONS FROM THE RECRUITMENT-STOCK-TEMP  
C RELATION (ARRAY DEV)
- C (4) REPLACEMNT OF THE FUNCTION LINKING LENGTH AFTER 4 GROWING SEASONS (L4)  
C TO POPULATION DENSITY BY INPUT VALUES FOR L4 (ARRAY OBLG)

C OUTPUT IS IN NUMBER OF FISH, KILOGRAMS & CENTIMETERS  
C ALL ARRAYS ARE DIMENSIONED TO PROVIDE YEARLY POPULATION STATISTICS  
C FOR 28 YEARS

C DIMENSION CORMAT(28),OBLG(28)  
C DIMENSION DEV(28)  
C DIMENSION TOTWT(28),RECORD(28,8,4)  
C DIMENSION RLG(3,8), RND(3,8),TEMP(28),RWT(3,8)  
C DIMENSION SURV(2,28,4)

C TOTWT(I)=TOTAL WEIGHT FISHERIES CATCH YEAR I  
C RECORD(I,J,1)=LENGTH FISH AGED J AT START YEAR I  
C RECORD(I,J,2)=NO FISH AGED J AT START YEAR I  
C RECORD(I,J,3)=NO FISH AGED J LOST IN YEAR I  
C RECORD(I,J,4)= WT. OF FISH AGED J CAUGHT IN YEAR I  
C RLG(1,J)= LENGTH FISH AGED J AT START OF YEAR  
C RLG(2,J)= LENGTH FISH AGED J AT END OF YEAR  
C RLG(3,J)= LENGTH FISH AGED J HALF WAY THRU YEAR  
C RND (1,J)= NO. FISH AGED J AT START OF YEAR  
C RND (2,J)= NO. FISH AGED J AT END OF YEAR  
C RND (3,J)= NO. FISH AGED J LOST IN YEAR  
C TEMP(1)= RATE OF TEMPERATURE INCREASE IN YEAR I  
C RWT(1,J)= WEIGHT OF FISH AGED J HALF WAY THRU YEAR  
C RWT(2,J)= WEIGHT OF FISH AGED J LOST IN YEAR  
C RWT(3,J)= WEIGHT OF FISH AGED J IN FISHERIES CATCH  
C SURV(K,I,J)= SURVIVAL RATE OF FISH AGED J IN YEAR I ACCORDING  
C TO SURVIVAL SCHEDULE K  
C CORMAT(I)=PERCENT 3-YEAR-OLDS MATURE IN YEAR I  
C DEV(I)=DEVIATION FROM STOCK TEMPERATURE RECRUITMENT RELATION IN YEAR I  
C OBLG(I)=LGTH. AFTER 4 GROWING SEASONS OF THE YEAR CLASS HATCHED IN YEAR I

745 FORMAT(2X,13,2X,F11.1)

743 FORMAT(2X,13,8F12.1)

DO 152 I=1,28

152 TOTWT(I)=0.

DO 153 I=1,28

DO 153 J=1,8

DO 153 K=1,4

```

153  RECORD(I,J,K) =0.
      DO 1 I=1,3
      DO 1 J=1,8
          RLG(I,J)=0.
          RNO(I,J)=0.
1      DO 2 I=1,2
          DO 2 J=1,8
2          RUT(I,J)=0.
          READ,RNM,RNPCPE,RNPYOY,IYRSW,LGOPT
          RNM= SURVIVAL RATE ASSUMING NO FISHING MORTALITY
          RNPCPE= CONVERSION FACTOR FROM CPE TO NO'S: MATURE FISH
          RNPYOY= CONVERSION FACTOR FROM CPE TO NO'S: RECRUITS
          IYRSW=YEAR WHEN SWITCH SURVIVAL RATE SCHEDULES
          LGOPT= INDICATOR OF MODE FOR GROWTH DETERMINATION (=0: FROM POPULATION
                  DENSITY; =1: FROM L4 VALUES IN 'DBLG')
          READ,(DBLG(I),I=1,28)
          READ,(CORMAT(I),I=1,28)
          READ,(SURV(1,I,J),J=1,4),I=1,28)
          READ,(SURV(2,I,J),J=1,4),I=1,28)
          READ,(TEMP(I),I=1,28)
          READ,(DEV(I),I=1,28)
          READ IN INITIAL NO'S AND LENGTHS AT AGE FOR EACH AGE GROUP
          READ,(RNO(1,I),I=1,8)
          READ,(RLG(1,I),I=1,8)
          APPLY CPE AND YOY SCALING FACTORS TO INITIAL CONDITIONS
          RNO(1,1)=RNO(1,1)*RNPYOY
          RNO(1,2)=RNO(1,2)*RNPYOY
          DO 7310 I=3,8
7310  RNO(1,I)=RNO(1,I)*RNPCPE
          APPLY SCALING FACTORS TO RECRUITMENT AND GROWTH FUNCTIONS
          RECCON=RNPYOY/RNPCPE**1.585
          RLGCN=.82715/RNPCPE
          ISRVSJ=1
          START YEARLY ITERATIONS
          DO 1000 INYR=1,28
          IYR=45+INYR
          IF(IYR.EQ.IYRSW)ISRVSJ=2
          DETERMINE BREEDING STOCK
          STK=RNO(1,3)*CORMAT(INYR)
          DO 10 I=4,8
          STK=STK+RNO(1,I)
          CONTINUE
10      DETERMINE RECRUITS YEAR I+1
          TEM3=2.3*DEV(INYR)
          TEM1=1.012*RECCON*(STK**1.585)
          TEM2=15850**TEMP(INYR)
          REC=TEM1*TEM2*EXP(TEM3)
          ASSIGN LENGTHS AND WEIGHTS AT MIDDLE AND END OF GROWING SEASON
          DO 20 I=1,8
          RECORD(INYR,I,1)=RLG(1,I)

```

```

RECORD(INYR, I, 2) = RND(1, I)
RLG(2, I) = 12.4 + .836 * RLG(1, I)
RLG(3, I) = (RLG(1, I) + RLG(2, I)) / 2.0
RWT(1, I) = .0000132 * (RLG(3, I)) ** 2.9302
CONTINUE

20 C
C   CALCULATE MORTALITY
DO 30 I=1.7
  I9=1
  IF(I9.LT.4)GO TO 32
  I9=4
32  RND(2, I) = RND(1, I) * SURV(ISRVSW, INYR, I9)
30  CONTINUE
RND(2, 0) = 0

C
C   CALCULATE NO.'S AND WT LOST
DO 40 I=1.8
  RND(3, I) = RND(1, I) - RND(2, I)
  RWT(2, I) = RND(3, I) * RWT(1, I)
  RECORD(INYR, I, 3) = RND(3, I)
40  CONTINUE

C
C   CALCULATE WEIGHT OF FISHERIES CATCH
DO 50 I=1.7
  I29=1
  IF(I29.LT.4)GO TO 52
  I29=4
52  TEM7 = SURV(ISRVSW, INYR, I29) * 1.11
  Z = -ALOG(TEM7)
  RWT(3, I) = RND(1, I) * (1 - TEM7) * RWT(1, I) * (Z - .11) / Z
  IF(SURV(ISRVSW, INYR, I29).EQ.RNM)RWT(3, I) = 0.0
  RECORD(INYR, I, 4) = RWT(3, I)
  TOTWT(INYR) = RWT(3, I) + TOTWT(INYR)
50  CONTINUE
RWT(3, 0) = 0.

C
C   DETERMINE LENGTH OF 1 YEAR OLDS AT START OF FOLLOWING YEAR
IF(LGOPT.EQ.1)GO TO 11852
STCK2 = RND(1, 1) * .8
DO 60 I=2.8
  STCK2 = STCK2 + RND(2, I)
  TEML3 = RLGCON * STCK2
  RL3 = 51.6 - 0.673 * EXP(TEML3)
  GO TO 11853
11852 RL3 = OBLG(INYR)
11853 DO 7829 I=1.3
  RTP = -14.8 + 1.2 * RL3
7829  RL3 = RTP
  CONTINUE
  RNWL1 = RL3
  IF(RNWL1.LT.15.2)RNWL1 = 15.2
DO 70 I=1.7
  I53=I+1
  RND(1, I53) = RND(2, I)
  RLG(1, I53) = RLG(2, I)
70  CONTINUE
RND(1, 1) = REC
RLG(1, 1) = RNWL1
1000 CONTINUE
PRINT, '
PRINT, ' ***** YEARS 47 - 74 *****'
PRINT, '
PRINT, ' ***** NO./YOY = ', RNPY0Y

```

```

PRINT,' '
PRINT,' ' ***** NO./CPE = ',RNPCPE
PRINT,' '
PRINT,' ' *****YEAR SURVIVAL RATES SWITCH = ',IYRSW
PRINT,' '
PRINT,' ' LENGTHS AT START EACH YEAR AGE GROUPS 1-8'
PRINT,' '
DO 601 I=1,28
K=46+I
WRITE(6,743)K,(RECORD(I,J,1),J=1,8)
601 CONTINUE
PRINT,' '
PRINT,' ' NOS AT START OF EACH YEAR AGE GROUPS 1-8'
PRINT,' '
DO 602 I=1,28
K=46+I
WRITE(6,743)K,(RECORD(I,J,2),J=1,8)
602 CONTINUE
PRINT,' '
PRINT,' ' NOS LOST EACH YEAR AGE GROUPS 1-8'
PRINT,' '
DO 603 I=1,28
K=46+I
WRITE(6,743)K,(RECORD(I,J,3),J=1,8)
603 CONTINUE
PRINT,' '
PRINT,' ' WT OF CATCH EACH YEAR AGE GROUPS 1-8'
PRINT,' '
DO 604 I=1,28
K=46+I
WRITE(6,743)K,(RECORD(I,J,4),J=1,8)
604 CONTINUE
PRINT,' '
PRINT,' ' TOTAL WEIGHT CATCH EACH YEAR'
PRINT,' '
DO 605 I=1,28
K=46+I
WRITE(6,745) K,TOTWT(I)
605 CONTINUE
STOP
END

```

APPENDIX B

```

C      WEYEZ IS A STOCHASTIC DYNAMIC PROGRAMMING MODEL FOR WALLEYE HARVEST
C      IN WESTERN LAKE ERIE
C
C      INTEGER T,T1
C      DIMENSION HAR(30)
C      DIMENSION V(20,30),S(30),A(10),B(30),P(10),U(30)
C      DIMENSION F(3),DM(3),SN(10),W(10)
C
C      MEAN WEIGHT DATA FOR EACH YEAR CLASS
C
C      DATA W/.15,.55,.98,1.4,1.79,2.21,4*3.15/
C
C      ADD DATA FILE TO RUNSTREAM
C
C      CALL OPENF(S,'WDF1')
C      FORMAT(4(I2,1X))
C      FORMAT(F3.0,1X,F4.2,1X,F3.0,1X,F4.2)
C      FORMAT(10(F2.0,1X))
C      FORMAT(10(F4.0,1X))
C      FORMAT(' ','EXP RATES FOR THIS RUN'/(10(F4.2,1X)))
C      FORMAT(' ','STOCK SIZES DEFINED FOR THIS RUN'/(10(F4.1,1X)))
C      FORMAT(' ','ALPHA AND P(ALPHA)'/(10(F4.2,1X)))
C      FORMAT(' ','CATCHABILITY COEF'/(3(F5.2,1X))/'NATURAL MORTALITY
C      1COEF'/(3(F5.2,1X))
C      FORMAT(6(F3.2,1X),F7.0)
C      FORMAT('0','FOR TIME',I2,'OPTIMAL HARVEST RATES ARE'/
C      1(10(F4.2,1X)))
C      FORMAT(10X,'VALUES FOR ABOVE HARVEST RATES'/(5(1X,E9.3)))
C
C      DATA INPUT
C      N1=NO. STOCK INTERVALS, N2=NO. EXPLOITATION INTERVALS,
C      N3=NO. ALPHA INTERVALS
C
C      READ(5,5)N1 ,N2,N3,T
C
C      S(1)=LOW STOCK SIZE, D1=STOCK SIZE INCREMENT,U(1)=LOW EXPLOITATION
C      EFFORT, D2=EXPLOITATION INCREMENT
C      READ(5,6)S(1),D1,U(1),D2
C
C      ALPHA VALUES(DT/T) AND PROBABILITIES OF EACH VALUE
C
C      READ(5,7)(A(I),P(I),I=1,N3)
C
C      INITIAL STOCK VALUES
C
C      READ(5,9)(V(T,I),I=1,N1)
C      FISHING CATCHABILITY, NATURAL MORTALITY( >=3 YR HAVE SAME VALUE),
C      AND CONVERSION FACTOR FOR CPE OF 3 AND OLDER TO ABSOLUTE DENSITY
C      READ(5,13)(F(I),I=1,3),(DM(I),I=1,3),C1
C
C      DETERMINE VALUES OF STOCK AND EXPLOITATION INTERVALS
C
C      DO 30 I=2,N1
C      S(I)=S(I-1)+D1
C      DO 35 I=2,N2
C
C      PRINT INPUT DATA
C
C      U(I)=U(I-1)+D2
C      PRINT 9,(S(I),I=1,N1)
C      PRINT 10,(U(I),I=1,N2)
C      PRINT 11,(A(I),I=1,N3),(P(I),I=1,N3)
C      PRINT 12,(F(I),I=1,3),(DM(I),I=1,3)

```

```

C
C      COMPUTATION LOOP
T1=T-1
B(1)=0.
DM1=EXP(-DM(1))
DM2=EXP(-DM(2))
DM3=EXP(-DM(3))
DO 200 M=1,T1
I=T-M
DO 100 J=1,N1
V(I,J)=-100.
DO 80 K=1,N2
F1=EXP(-F(1)*U(K))
F2=EXP(-F(2)*U(K))
F3=EXP(-F(3)*U(K))
SN(1)=S(J)*C1
SN(2)=SN(1)*F1*DM1
SN(3)=SN(2)*F2*DM2
DO 45 L=4,10
SN(L)=SN(L-1)*F3*DM3
Z=SN(1)*(1-F2*DM1)*0.5*(W(1)+W(2))*F(1)*U(K)/(F(1)*U(K)+DM(1))
Z=Z+SN(2)*(1-F2*DM2)*0.5*(W(2)+W(3))*F(2)*U(K)/(F(2)*U(K)+DM(2))
H1=Z
DO 65 LL=3,10
Z=Z+SN(LL)*W(LL)*(1-F3)
H1=H1+SN(LL)*(1-F3*DM3)*0.5*(W(LL)+W(LL+1))*F(3)*U(K)/(F(3)*U(K)
1+DM(3))
DO 60 L=1,N2
X=325*(SN(LL))*0.505*(15850**A(L))
X=X/D1
IY=INT(X)+1
Y=IY
WTEMP=X-Y-1
IF(Y.LT.N1)GO TO 50
V1=V(I+1,N1)
GO TO 55
50  V1=V(I+1,IY)+WTEMP*(V(I+1,IY+1)-V(I+1,IY))
55  Z=Z+P(L)*W1/8
60  CONTINUE
65  CONTINUE
IF(Z.LE.V(I,J))GO TO 80
V(I,J)=Z
HAR(J)=H1
B(J)=U(K)
CONTINUE
80  CONTINUE
100 PRINT 15,1,(B(K),K=1,N2)
PRINT 16,(HAR(K),K=1,N2)
CONTINUE
200 STOP
END

```

