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COMPUTER SIMULATION OF THE POPULATION DYNAMICS OF LAKE WHITEFISH IN NORTHERN LAKE MICHIGAN

By

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ABSTRACT

COMPUTER SIMULATION OF THE POPULATION DYNAMICS OF LAKE WHITEFISH IN NORTHERN LAKE MICHIGAN

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The effects of the present trap and gill net commercial fishery on a population of lake whitefish (Coregonus clupeaformis) in northern Lake Michigan were investigated. A mathematical model was developed to simulate the current fishery and investigate possible management strategies in relation to sustainable yield and annual yield variability. The model consisted of an age/size structured, dynamic pool model incorporating a stock-recruitment function subject to environmental variability. Trap and gill net selectivity functions specified the fishing mortality rates operating on each cohort.

Three scenarios, representing possible directions of the fishery, were investigated. The first scenario involved a multi-gear fishery with gear-specific fishing mortality rates as manageable (controllable) inputs. The second and third scenarios investigated the possibilities of either an exclusive trap net fishery or an exclusive gill net fishery with fishing mortality rates, minimum size limits (trap net simulations) and mesh size restrictions (gill net simulations) as controllable inputs. Combinations of the controllable inputs were identified which resulted in a large sustainable yield and a low level of annual variability.

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INTRODUCTION

The lake whitefish (*Coregonus clupeaformis*) is a historically important, commercially utilized species in Lake Michigan. With most of the other valuable species now either extinct or seriously depleted, the whitefish has become even more important to the commercial fishing industry. Over two million kilograms have been harvested annually from Lake Michigan since 1971 (Baldwin et. al. 1979). Increased demand for whitefish from a Chippewa and Ottawa Indian treaty fishery coupled with a large state-licensed commercial fishery has resulted in a significant buildup of fishing effort. Fisheries managers are concerned that the present level of exploitation is excessive (Patriarche 1977). A collapse of the whitefish stocks would be devastating to the Lake Michigan commercial and treaty fishery. The objectives of this study were to analyze the vital statistics of the lake whitefish populations in northern Lake Michigan, and to develop and utilize a simulation model to investigate the effects of the present fishery on the long term yield and stability of the system and to explore the effectiveness of various other management strategies.

The lake whitefish is widely distributed over the northern half of North America, including all of the Great Lakes (Scott and Crossman 1973). In Lake Michigan, they inhabit the cool water at depths of 10 to 60 meters. Whitefish grow as large as 10 kilograms, but average about 1 kilogram in the lake Michigan commercial catch. The adult diet consists primarily of benthic insect larvae, small molluscs and amphipods (Koelz 1929). Lake whitefish spawn in November in water less than 10 meters over rock and sand (Scott and Crossman 1973).

The study area consisted of the northeastern section of Lake Michigan (Figure 1). Several broad lake habitat types are represented within the area, ranging from the sharply, sloping shoreline and deep water (>60 meters) around the Leleenau Peninsula (Leland) to the relatively shallow (< 40 meters) and productive north shore area. A large island complex is located in the central portion of the study area.

Scheerer (1982) identified at least three separate stocks of whitefish within the study area (he defined a stock as a manageable unit of reproductively isolated fish). One inhabits the waters off the western side of the Leleenau Peninsula, another near the Beaver Island complex and one along the north shore of the lake. He estimated a fall 1980 biomass of 1.4 million kilograms of whitefish in the north shore population.

A trap net fishery operates at depths of less than 30 meters and only during the open water season (approx. April through December). A gill net fishery operates during both the open water and ice-cover seasons and at depths of up to

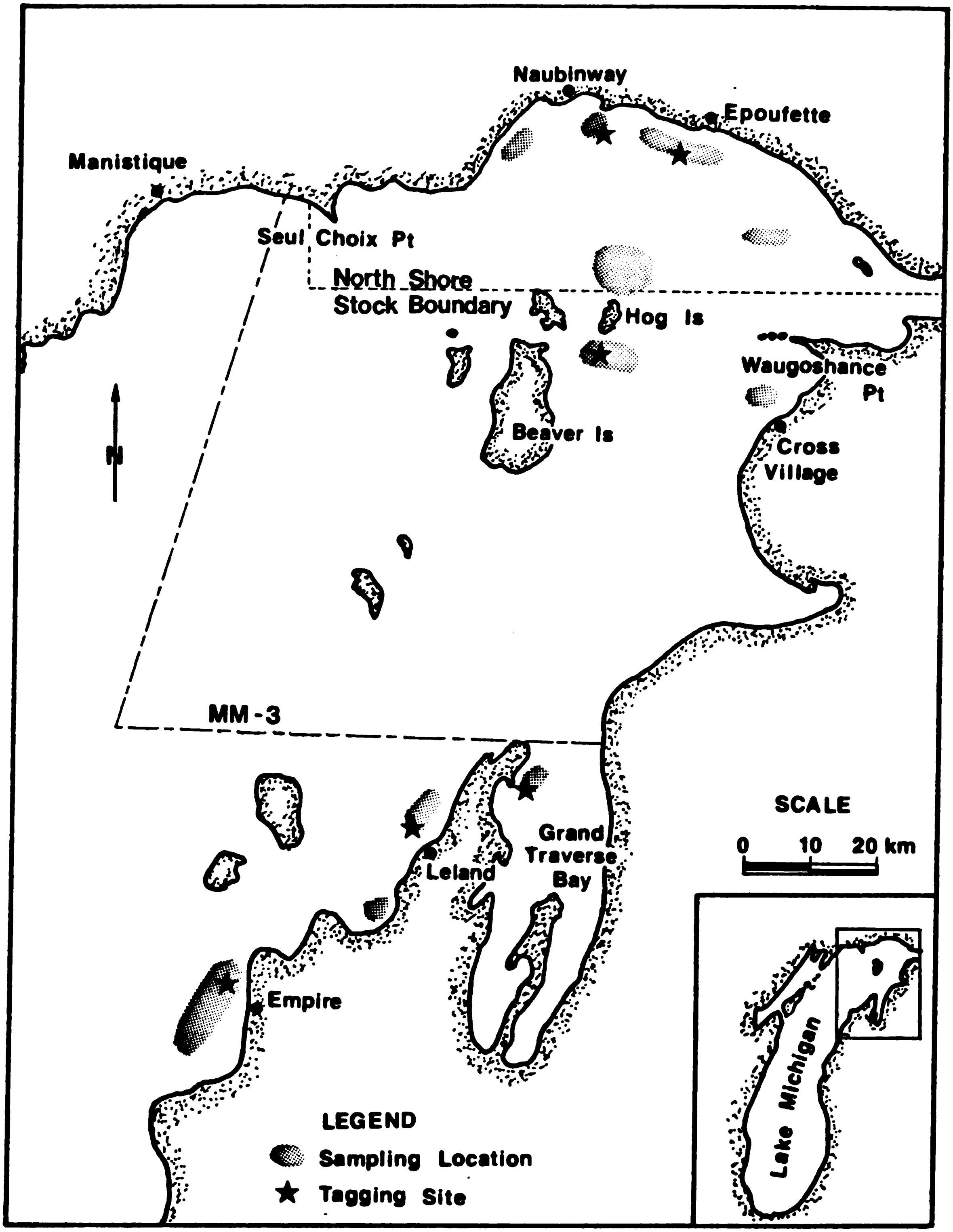


Figure 1. Map of the study area with sampling and tagging locations.

50 meters and deeper. The season is closed during the month of November (spawning season) for both gear types. Most of the gill nets and the trap net pots use a 114 mm stretched mesh net.

The north shore population has supported a highly productive commercial fishery operating out of the ports of Naubinway, Epoufette, Brevort and St. Ignace. The large expanse of moderately shallow water (10-40 meters) provides for the high production of benthic invertebrates required by adult whitefish. Several whitefish population studies have been conducted on this north shore stock (Roelofs 1958, Jensen 1976, Patriarche 1977, Scheerer 1982). The extensive north shore population data from these studies, combined with unpublished reports from the Michigan Department of Natural Resources, represented the most complete data set for any of the stocks within the study area. The simulation model was developed and parameterized specifically for the north shore population. Data were collected from other areas for comparative purposes.

The annual commercial harvest of lake whitefish in Lake Michigan has fluctuated dramatically (Figure 2). The recent history (1948-1981) of annual whitefish production in statistical district MM-3 (Smith et. al. 1961 - refer to Figure 1) is displayed in Figure 3a. Pre - 1948 production peaks occurred in the 1880's, the late 1920's and the 1940's. The recent period of high production follows the years of 1957 - 1960 when there was essentially no commer-

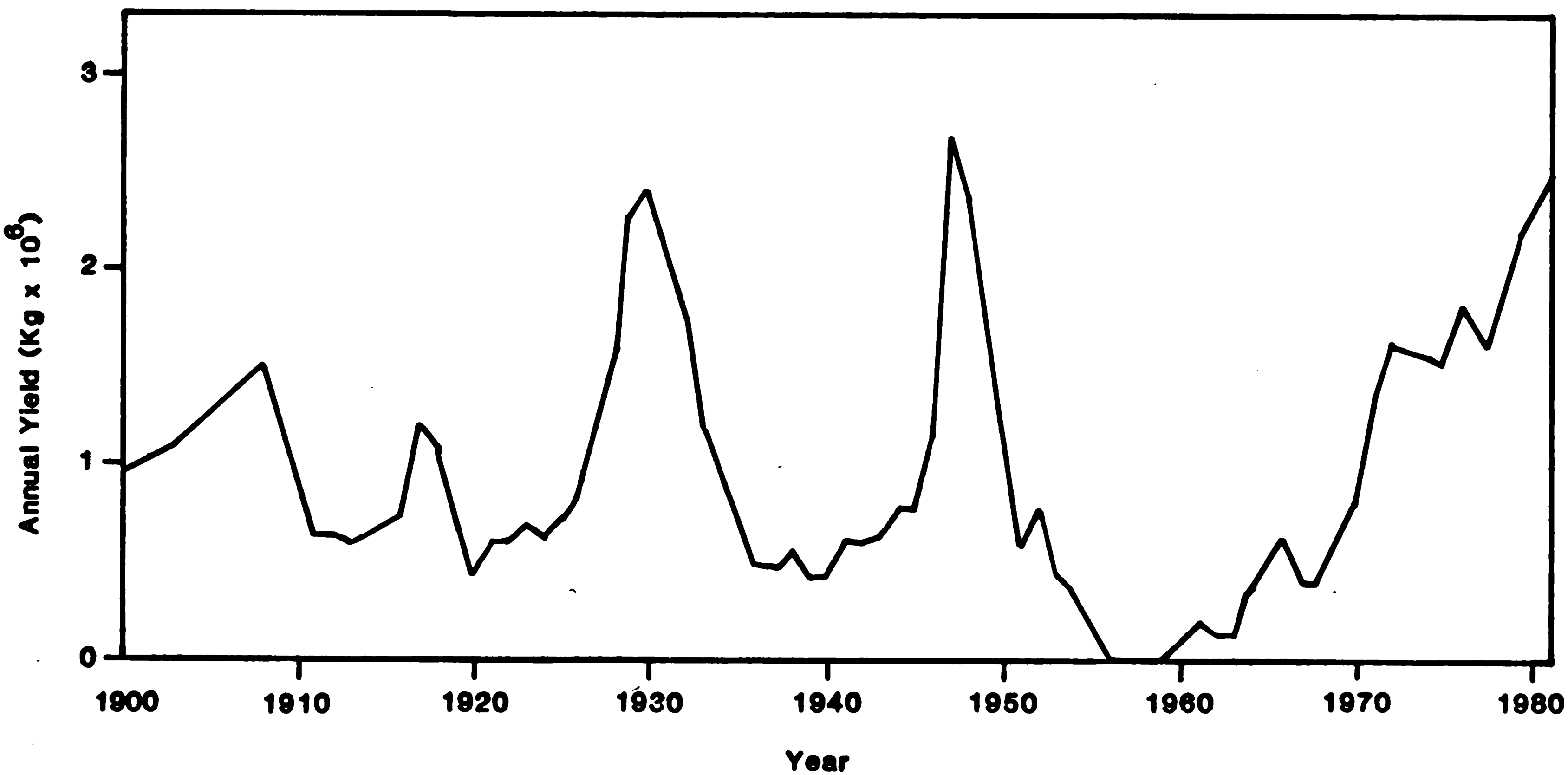
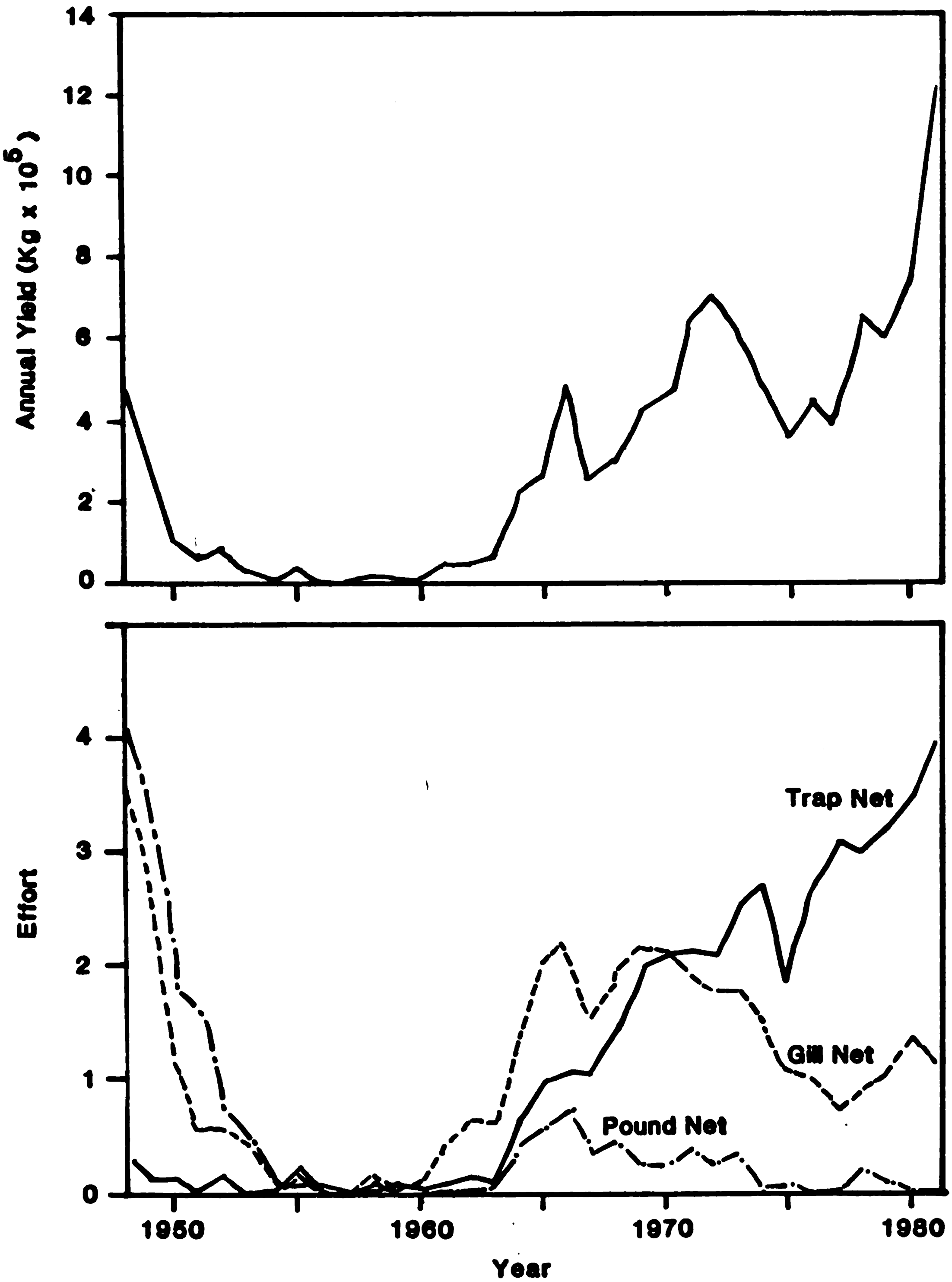


Figure 2: Commercial harvest of lake whitefish in Lake Michigan from 1900-1981 (Baldwin, et. al. 1979).

cial production. Overexploitation, exotic species introduction, and high year class strength variability have been implicated in these fluctuations. (Smith 1968, Wells and McLain 1973).

The recent increase in lake whitefish abundance can be attributed to a decrease in sea lamprey predation (Wells and McLain 1973). This lower lamprey predation rate is the result of effective sea lamprey control and the increased abundance of lake trout which is the favored target of the lamprey.

The recent trends in fishing effort by the major gear types are displayed in Figure 3b. All have shown increases since the 1960's, except for pound net effort, which has recently dropped to zero in the district. A required conversion from gill nets to trap nets for state-licensed commercial fishermen in the 1970's has resulted in an increase in trap net effort and a decrease in gill net effort. Currently, the primary source of gill net effort is represented by the treaty fishery.



Figures 3a and 3b. Commercial harvest (Fig. 3a) and effort (Fig. 3b) for lake whitefish in statistical district MM-3 (Smith et. al. 1961) of Lake Michigan, 1948-1981. Units of effort are thousands of lifts of trap and pound nets and millions of feet of gill net lifted. (Data from the Great Lakes Fishery Lab, United States Fish and Wildlife Service, Ann Arbor, Michigan).

MODEL DEVELOPMENT

An adequate mathematical model of the dynamics of this system requires the incorporation of several important biological phenomona, characteristic of lake whitefish populations in general. For example, the existence of highly variable year class strength has been observed in many populations of whitefish. Several mechanisms have been suggested which might generate these fluctuations, but there has been no general consensus of which may be most important. Miller (1952) suggested that winds at spawning time are important in determining year class strength for whitefish in several lakes in Alberta, Canada. Christie (1963) suggested that air temperatures at the time of spawning and hatching are important factors. Lawler (1965) concluded that prolonged incubation periods are crucial for good year class strength in whitefish in their extreme southern range (Lake Erie). All of these factors could potentially generate variability in recruitment of northern Lake Michigan whitefish populations. The interaction of this variability and the level of fishing is of interest to lake whitefish managers and commercial fishermen.

The influence of environmental variability on the stability of fish yield has been investigated by several authors, using widely different approaches. Variability has been incorporated into stock-recruitment models (Ricker 1958, Allen 1973, Walters 1975), population growth models (Beddington and May 1977, May et. al. 1978), and age-structured models (Getz and Swartzman 1981, Horwood and Sheperd 1981). All of the authors have concluded that there can be an inherent tradeoff between the mean and the variance of yield, and that this tradeoff is an important consideration in the management of a fluctuating population.

The relative influence of spawning stock density on the recruitment of lake whitefish is also an important question. Lawler (1965) could not explain year class variability on the basis of spawning population size in Lake Erie. However, Christie (1963) suggested that spawning stock density did play an important role in determining recruitment, especially in years with unfavorable environmental conditions. The relative contribution that both density dependent and density independent factors have towards determining recruitment should be an important component of a lake whitefish management model.

The contrasting ways in which the two different gear types affect the size and age structure of the population is another important consideration in developing the model. Trap nets harvest fish over a much broader range of size and ages than do the relatively more selective gill nets. Each gear type produces a different fishing mortality on each cohort.

In addition to incorporating the important biological characteristics into the model, specific manageable inputs must be identified. Closed seasons, gear limitations, limited entry and minimum size limits have commonly been used in lake whitefish management. Some regulations are designed to control fishing mortality, others are designed to protect certain segments of the population from harvest, such as immature fish or spawning fish. Several of these regulations can be generalized by controlling the gear-specific fishing mortality rates in the model.

With these considerations in mind, a continuous time, age/size-structured, dynamic pool model incorporating a stock-recruitment function subject to random density-independent variation was developed. Trap and gill net selectivity curves specify instantaneous fishing mortality rates for each cohort. The model allows for the manipulation of four controllable inputs:

1. trap net fishing mortality rate
2. gill net fishing mortality rate
3. trap net minimum size limit
4. gill net mesh size

There is no minimum size limit for gill nets. The size range of fish harvested by gill nets can be controlled by the mesh size restriction.

Appendix 1 is a glossary of variable names used in the text. The specific components of the model are presented in the following sections.

GROWTH

Individual body growth is modeled using a modified (t_0=0) von Bertalanffy growth equation (von Bertalanffy 1938):

$$l_i(t) = L_\infty\,(1-\exp(-Kt)) \qquad (1)$$

where,

$l_i(t)$ = length of fish in cohort i at time t

L_∞ = asymptotic length parameter

K = growth coefficient

Weights are calculated from the standard length-weight equation (Ricker 1975):

$$w_i(t) = a\ l_i(t)^b \qquad (2)$$

where,

$w_i(t)$ = weight of fish in cohort i at time t

a,b = length-weight parameters

MORTALITY

The decline in numbers of fish in a cohort over time is assumed to be a negative exponential function (Ricker 1975). The total mortality rate is separated into three components: natural, trap net fishing and gill net fishing. The function can be written in the form of a differential equation using instantaneous mortality rates:

$$\frac{dN_i}{dt} = -(F_{T,i} + F_{G,i} + M_i)\ N_i \qquad (3)$$

where,

N_i = number of fish in cohort i

$F_{T,i}$ = instantaneous trap net mortality rate operating on cohort i

$F_{G,i}$ = instantaneous gill net fishing mortality rate operating on cohort i

M_i = instantaneous natural mortality rate operating on cohort i

The specific trap and gill net mortality rates operating on a cohort are direct functions of fish size and gear selectivity. Fortunately, the selectivity curves for whitefish have been worked out by McCombie and Fry (1960) for gill nets and Eshenroder et. al. (1980) for trap nets.

McCombie and Fry estimated the relative selectivity of gill nets in terms of the ratio of fish girth to mesh perimeter. First, a length-girth relationship must be established:

$$g_i(t) = A + B\, l_i(t) \tag{4}$$

where,

$g_i(t)$ = girth of fish in cohort i at time t

A,B = length-girth parameters

The relative efficiency can then be calculated as a function of cohort girth and gill net mesh size with a log-normal selectivity equation:

$$RE_{G,i}(t) = C_G[\sigma_G \sqrt{2\pi}\, g_i(t)/m_G]^{-1}[\exp(-(\ln(g_i(t)/m_G) - \mu_G)^2/2\sigma_G^2)] \tag{5}$$

where,

$RE_{G,i}(t)$ = relative efficiency of gill nets on cohort i at time t (ranges from 0.00 to 1.00)

m_G = gill net mesh perimeter (equal to 2x stretched mesh measurement)

μ_G = mean of the log-normal selectivity curve

σ_G = standard deviation of the log-normal selectivity curve

C_g = constant (required to adjust the range of relative efficiency to 0.00 to 1.00)

The cohort-specific gill net fishing mortality rate is calculated by multiplying the relative efficiency times an apical instantaneous fishing mortality rate:

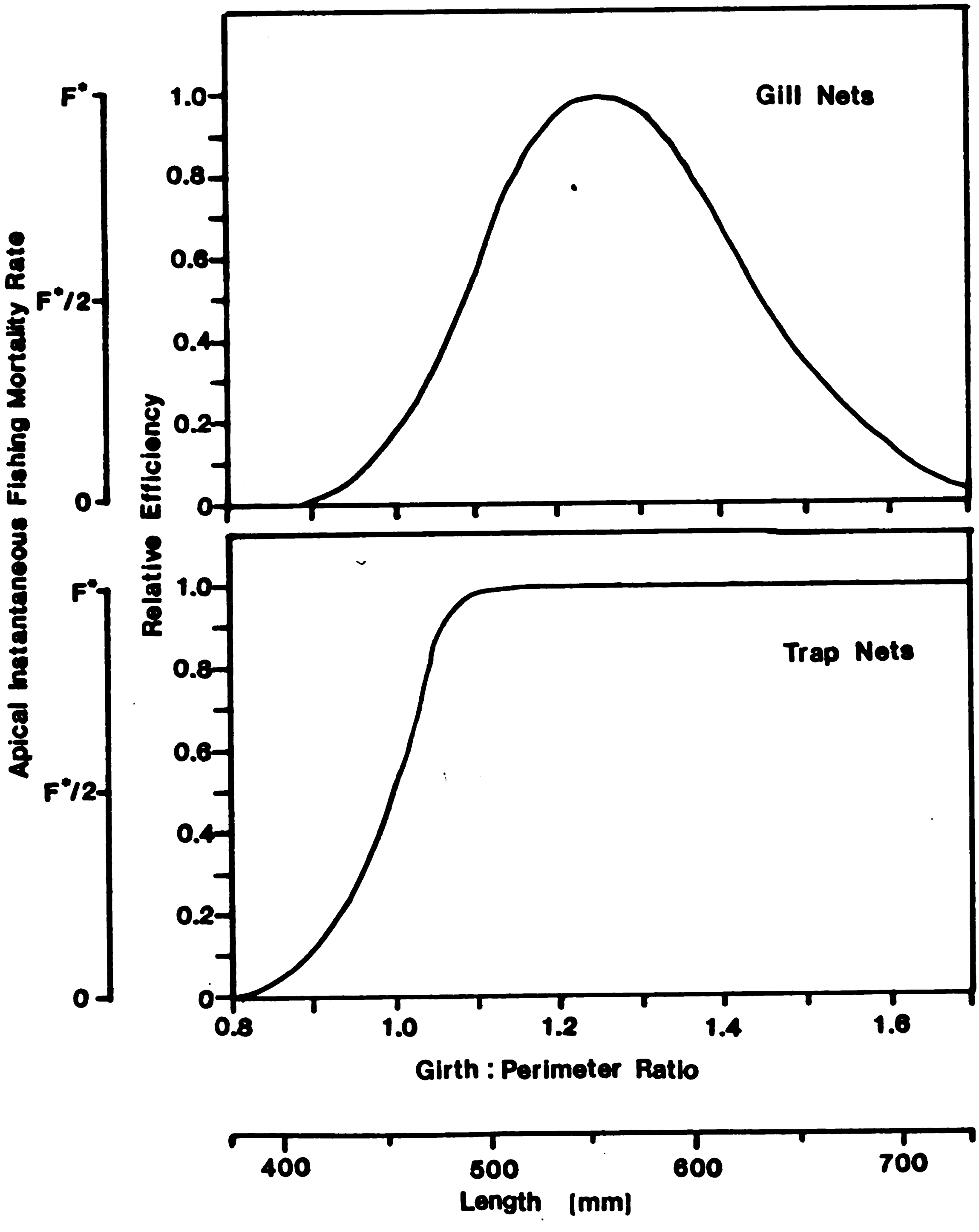
$$F_{G,i}(t) = RE_{G,i}(t)\ F_G^* \qquad (6)$$

where,

$F_{G,i}(t)$ = specific instantaneous gill net fishing mortality rate operating on cohort i at time t

F_G^* = apical instantaneous gill net fishing mortality rate (controllable input)

Apical instantaneous fishing mortality is defined as the instantaneous fishing mortality rate at the point of maximum efficiency on the gear selectivity curve. Figure 4a illustrates the shape of the gill net selectivity curve, both in terms of a girth to perimeter ratio and and actual fish length. Maximum efficiency occurs at a girth to perimeter ratio of 1.26 and a fish length of 555 millimeters (for a 114 mm stretched mesh gill net). This is equivalent to saying that a gill net is most efficient for whitefish when the girth of the fish is 1.26 times as large as the perimeter of an individual mesh opening. Fish with girths either larger or smaller than this value will be captured with less efficiency. The specific instantaneous fishing mortality rate $F_{G,i}(t)$ will be exactly equal to the apical instantaneous fishing mortality rate F_G^*



Figures 4a and 4b. Gill net selectivity curve (Fig. 4a) from McCombie and Fry (1960) and trap net selectivity curve (Fig. 4b) from Eshenroder et. al. (1980) in terms of girth to perimeter ratio and actual fish length for whitefish in northern Lake Michigan. Actual fish length scale is for a 114 mm stretched mesh net.

when the cohort has fish with girths 1.26 times the perimeter of the mesh opening. At all other girths, $F_{G,i}(t)$ will be less than F_G^*.

Cohort-specific trap net mortality is calculated in the same manner. Eshenroder et. al. (1980) also used the girth to perimeter ratio concept to determine trap net selectivity. Although not presenting a specific functional relationship in their paper, one of the authors (Doug Jester, personal communication) suggested fitting the following equation to their data:

$$RE_{T,i}(t) = [(g_i(t)/m_G)^{**}C_1]/[(C_1^{**}C_2) + (g_i(t)/m_T)^{**}C_1] \tag{7}$$

where,

$RE_{T,i}(t)$ = relative efficiency of trap nets on cohort i at time t (ranges from 0.00 to 1.00)

m_T = trap net mesh perimeter (equal to 2x stretched mesh measurement)

C_1, C_2 = selectivity curve parameters

The specific instantaneous trap net mortality can then be calculated:

$$F_{T,i}(t) = RE_{T,i}(t)\ F_T^* \tag{8}$$
$$= 0 \qquad \text{if} \quad l_i(t) < MSL$$

where,

$F_{T,i}(t)$ = specific instantaneous trap net fishing mortality rate operating on cohort i at time t

F_T^* = apical instantaneous trap net fishing mortality rate

MSL = trap net minimum size limit

The trap net selectivity curve is illustrated in Figure 4b. Maximum efficiency occurs at a girth:perimeter ratio greater than 1.10 and at fish lengths greater than 500 mm, for a 114 mm stretched mesh trap net. The specific instantaneous fishing mortality rate, $F_{T,i}(t)$, equals the apical instantaneous fishing mortality rate, F_T^* , at girth:perimeter ratios greater than 1.10 and fish lengths greater than 500 mm.

Maximum efficiency for trap nets occurs at a smaller girth:perimeter ratio than for gill nets (1.10 vs. 1.26). Eshenroder et. al. (1980) suggest that this disparity is probably related to different capture mechanisms. Gill nets must retain against more of an escapement struggle than fish impounded in a trap net. This behavioral difference was substantiated by field observations within the study area. While a small percentage of whitefish were gilled during a trap net lift, the vast majority were passively retained within the lifting pot. In contrast, whitefish struggled greatly to escape during a gill net lift. This active motion allows whitefish with a girth:perimeter ratio of slightly greater than 1 to pass through the gill net's mesh. The selectivity curves in Figure 4 illustrate that the relative efficiency at a girth:perimeter ratio of 1.00 is only 15% for gill nets, but near 50% for trap nets. Interestingly, trap nets are also significantly efficient for fish small enough to easily pass through the mesh (girth:perimeter <1.00). Again, this is due to the relatively passive nature of whitefish in trap nets.

Actual numbers of fish in a cohort are calculated by integrating Equation 3:

$$N_i(t) = N_i(t_R) - \int_{t_R}^{t} -(F_{T,i} + F_{G,i} + M_i)\, N_i \, dt \qquad (9)$$

where,

$N_i(t)$ = number of fish in cohort i at time t

t_R = time at recruitment

RECRUITMENT

The recruitment submodel was developed to include both density-dependent and density-independent factors. The Ricker stock-recruitment function presented by Walters (1975) was used:

$$R = \alpha S \exp(-\beta S) \exp(v) \qquad (10)$$

where,

R = number of recruits

S = spawning biomass

α, β = fitting parameters

v = independent random variable, normally distributed with a mean of 0.0 and a standard deviation of σ_R

This approach does not require the identification of the specific abiotic mechanism(s) which affect recruitment. Instead, an empirical measure of variability σ_R, is calculated from existing recruitment data. The log-normal distribution of the error term exp(v), is common to a wide variety of fish populations (Allen 1973, Walters 1975, Peterman 1981) and is characterized by a large number of average and slightly below average recruitments, with an occasional production of a very large year class. The multiplicative nature of exp(v) produces higher levels of variability at greater spawning stock densities.

YIELD

The rate of yield accumulation is assumed to be a direct function of the instantaneous fishing mortality rate and the number of fish present (Beverton and Holt 1957) and can be represented by the following differential equations:

$$\frac{dY_{T,i}}{dt} = F_{T,i} N_i w_i \qquad (11)$$

$$\frac{dY_{G,i}}{dt} = F_{G,i} N_i w_i \qquad (12)$$

where,

$\frac{dY_{T,i}}{dt}$ = rate of trap net yield accumulation for cohort i

$\frac{dY_{G,i}}{dt}$ = rate of gill net yield accumulation for cohort i

The actual yield is calculated by integrating the differential yield equations:

$$Y_{T,i}(t) = \int_{t_R}^{t} F_{T,i} N_i w_i \, dt \qquad (13)$$

$$Y_{G,i}(t) = \int_{t_R}^{t} F_{G,i} N_i w_i \, dt \qquad (14)$$

where,

$Y_{T,i}(t)$= trap net yield from cohort i at time t

$Y_{G,i}(t)$= gill net yield from cohort i at time t

Yield for the entire population is calculated by summing the contributions from each cohort:

$$Y_{POP}(t) = \sum_{i=0}^{I_{MAX}} (Y_{T,i}(t) + Y_{G,i}(t)) \tag{15}$$

where,

$Y_{POP}(t)$ = total population yield at time t

I_{MAX} = maximum age attained

COMPUTER IMPLEMENTATION AND SIMULATION ORGANIZATION

The continuous time differential equations are solved by numerical integration. A simple predictor-corrector technique is used consisting of Euler's formula and the trapezoidal rule (Manetsch and Park 1981). The Euler formula makes a rough prediction of the value of the integral at relatively small steps of time (Δt) and then corrects the answer by the trapezoidal rule:

Predictor Step - Euler Formula

$$N_e(t + \Delta t) = N(t) + [f(N(t))]\,\Delta t \qquad (16)$$

Corrector Step - Trapezoidal Rule

$$N(t + \Delta t) = N(t) + \Delta t/2[f(N_e(t + \Delta t)) + f(N(t))] \qquad (17)$$

where,

Δt = time step

$N_e(t + \Delta t)$ = rough prediction

$N(t + \Delta t)$ = correction

$f(N(t))$ = differential equation to be solved (e.g. $\frac{dN_i}{dt}$, $\frac{dY_{T,i}}{dt}$, $\frac{dY_{G,i}}{dt}$)

The accuracy of this numerical integration depends on the size of Δt: the smaller the time step, the more accurate the solution for the range of Δt's of interest. A tradeoff exists between the size of Δt and computer time, with the smaller time steps being more expensive. An appropriate Δt is chosen which results in a predetermined level of accuracy (see Parameter Estimation section).

The simulation model is organized to calculate yield at annual intervals. At the end of each simulated year, yields are calculated (Equation 15), spawning biomass is determined (Equation 18), the resulting recruitment is computed (Equation 10) and the cohort integer age is updated.

$$S = \sum_{i=0}^{I_{MAX}} N_i(t)\ w_i(t) \qquad \text{iff } l_i(t) \geq l_M \tag{18}$$

where,

S= spawning biomass

l_M= length at maturity

This process runs the entire length of the simulation, at which time the mean and coefficient of variation of yield are calculated:

$$\overline{Y} = \sum_{n=1}^{n_{MAX}} Y_n \ / \ n_{MAX} \tag{19}$$

where,

$\overline{Y}$= mean annual yield

Y_n= yield in year n

n_{MAX}= simulation run length (number of years)

and,

$$CV = \sqrt{\sum_{n=1}^{n_{MAX}} (Y_n - \overline{Y})^2 / (n-1)} \; / \; \overline{Y} \tag{20}$$

where,

CV= coefficient of variation of yield

The first twenty simulated years are not included in the calculation of these descriptive statistics in an attempt to "wash out" any effect the initial conditions may have on the long term values. For example, consider a simulation which produces a long term yield much smaller than the yield possible in the short run. The inclusion of the early annual yields would aberrantly influence the calculation of mean annual yield. Although the short term behavior of the model may be of considerable interest, the primary objective of this study was to investigate the long term sustainable yield and stability. The short term model behavior could provide estimates of the yield possible in the near future, but would not provide any insight into the <u>sustainablity</u> of the yield.

The stochastic recruitment factor, v, is randomly generated from a normal distribution with a mean of zero and a standard deviation of σ_R. An inverse transformation technique (Manetsch and Park 1981) is used to generate these random numbers.

The coefficient of variation, (CV), was selected as the most appropriate statistic to describe the yield variability. Although standard deviation was considered, it does not take into account the relative magnitude of annual yield. For example, a high standard deviation at a low mean annual yield would have a more "noticeable" effect and impact on the commercial fishery than would a high standard deviation at a high mean annual yield. The coefficient of variation, however, does relate the magnitude of variability to the mean.

The model was implemented in Fortran 77 on a Cyber 750, Control Data Corporation computer. The program prints annual statistics and an end-of-simulation summary (Appendix 2).

PARAMETER ESTIMATION

The data used to parameterize the model came from several sources. Field data collected from October 1980 to June 1982 (Table 1) were used for many of the estimates. Paul Scheerer, an MSU graduate student also involved in this study, analyzed much of the data and estimated many of the population statistics. Other sources of information included data from the fisheries literature, the Michigan Department of Natural Resources and the United States Fish and Wildlife Service. Data from the north shore population were used to parameterize the model. Data from other areas of the lake were collected for comparative purposes.

FIELD METHODS

During the 1980 and 1981 closed season (November 1 - November 30), 3239 whitefish were tagged and released. The majority of the fish were tagged in the Naubinway-Epoufette area (2207), and the Leland-Empire area (532), with fewer numbers tagged near Beaver Island (19) and Grand Traverse Bay (163) (Table 1). Several commercial fishermen provided their time, nets, boats and expertise during the tagging operations. The fish were captured in 114 millimeter stretched mesh commercial trap nets. Each fish was measured for length, tagged with Floy FT-1 dart tags in 1980, and Floy FD-68C anchor tags in 1981, directly below the dorsal fin, then released. A $1.00 reward was offered for each tag returned and considerable contact with fishermen was made throughout the study to encourage the return of tags.

Table 1. Sampling dates, locations, and numbers of lake whitefish, 1980-1982.

Port	Date	Sample Type	N
	North Shore Area		
Naubinway	10/29/80	SLW	513
Naubinway	11/04/80	Tagged	1683
Epoufette	06/29/81	SLW	107
Epoufette	08/24/81	SLW	264
Epoufette	08/25/81	SLWF	36
Naubinway	10/17/81	SLW	170
Epoufette	10/24/81	SLW	161
Naubinway	11/03/81	Tagged	1024
Epoufette	05/17/82	SLW	263
Epoufette	05/17/82	GL	86
Epoufette	05/18/82	SLW	63
	Leland Area		
Leland	10/29/80	SLW	62
Leland	10/30/80	SLW	52
Leland	11/07/80	Tagged	415
Leland	06/15/81	SLW	81
Leland	08/27/81	SLW	94
Leland	10/21/81	SLW	134
Leland	10/22/81	SLW	110
Leland	11/02/81	Tagged	117
Leland	05/20/82	SLW	111
Leland	05/24/82	SLWG	14
Leland	05/24/82	SLW	107
Leland	05/24/82	SLWG	11
Leland	05/24/82	SLW	16
	Beaver Island Area		
Beaver Island	11/05/80	Tagged	19
Beaver Island	06/16/81	SLW	219
Charlevoix	05/18/82 05/19/82	SLW	169
	Grand Traverse Bay Area		
Northport	06/14/81	Tagged	163
Northport	06/14/81	SLW	140

S = scale sample, L = length, W = weight, G = girth, F = fin rays

The commercial trap net catch was sampled for length, weight, and age composition from October 1980 through June 1982 (Table 1). Total length was measured to the nearest 5 millimeters and weight to the nearest 10 grams. A scale sample was removed from the area midway between the dorsal fin and the lateral line.

Scale aging techniques were used to determine the age of each fish. Scales were magnified 22x on a Bell and Howell ABR-1020 microfiche reader. Crossing over on the posterio-lateral radius and disruptions of circuli were the primary criteria used for distinguishing annuli (Van Oosten 1923). Scales proved to be reliable estimators of age (Scheerer 1982). A ninety-four percent agreement was found between ages determined from fin ray sections and ages determined from scales (n=36). There was an 82% agreement between 192 scales read by both principal scale readers. Ricker (1975) considers an 80-90% agreement to be acceptable.

PARAMETER ESTIMATES

Scheerer (1982) calculated mean lengths from scales sampled during this study (Table 2). The values for lengths at ages one and two may be unrealistically high according to Scheerer, because of the back calculation technique he used. Therefore, only ages 3-10 were used in the estimation procedure. A nonlinear least squares regression method was used to estimate the von Bertalanffy growth parameters. The following values were calculated:

Table 2. Mean lengths of lake whitefish in northern Lake Michigan estimated by Scheerer (1982).

Age	Length
1	*334 millimeters
2	*390
3	430
4	455
5	482
6	525
7	570
8	646
9	653
10	666

*Lengths at ages 1 and 2 are probably unrealistic (Scheerer 1982) and are not used in the analysis.

L_∞=713.8 mm and K=0.254 (with t_0 fixed at zero).

The length-weight relationship parameters were estimated by Scheerer to be a = 4.24×10^{-9} and b = 3.12. This converts length in millimeters to weight in kilograms.

Scheerer calculated mortality rates by a mark-recapture analysis. Instantaneous natural mortality (M) was estimated at 0.368 and instantaneous fishing mortality (all gear types) at 0.861. The trap and gill net components of the fishing mortality can be calculated by determining the relative proportion of fish harvested by each gear type. Trap nets accounted for 65% and gill nets accounted for 35% of the total whitefish harvest in 1981 (unpub. data Michigan DNR). This produces estimates of instantaneous trap net mortality of 0.560 (65% of 0.861) and instantaneous gill net mortality of 0.301 (35% of 0.861). The apical instantaneous fishing mortalities associated with these rates were calculated iteratively. Successive one year simulations, using 1980 initial conditions, were made using various combinations of apical trap and gill net mortality rates. These trial simulations continued until a set of apical rates produced instantaneous rates that converged on the actual 1981 fishing mortality rates. ($F_T^* = 0.654$ and $F_G^* = 0.554$).

The length-girth parameters were estimated to be A = -32.98 and B = 0.5777 by simple linear regression. Initial population levels (Table 3) were calculated by Scheerer.

The gill net selectivity curve parameters are directly from McCombie and Fry (1960):

Table 3. Population estimates of lake whitefish by age class in November, 1980 in northern Lake Michigan (Scheerer 1982).

Age	Number
3	1,272,535
4	365,906
5	16,632
6	0
7	3,326
8	0
9	0
10	3,326
Total	1,663,207

$\sigma_G = 0.1184$ and $\mu_G = 0.2303$

(0.0514 and 0.100 when using base 10 logarithms).

The parameter C_G was a constant multiplier used to adjust the function to a 0.00 to 1.00 scale.

The trap net selectivity function parameters were estimated by non-linear least squares regression from the data presented in Eshenroder et. al. (1980):

$C_1 = 0.9879 \qquad C_2 = 25.43$

The recruitment parameters were perhaps the most difficult to estimate because of a lack of direct measures of spawning stock size and absolute recruitment. These values were estimated by the indirect technique detailed in Appendix 3. Briefly, the technique utilizes the principle that stock size is directly proportional to catch per unit effort (CPE) (Ricker 1975). Spawning biomass for each year is calculated from the average trap net CPE (kgs/lift) during that year. The constant that linearly relates the two was estimated from mark-recapture data. This method assumes that only the mature portion of the population is being estimated. Fortunately, the current trap net minimum size limit of 432 mm is roughly equivalent to the length at maturity (Scheerer 1982).

Absolute recruitment was estimated by calculating the partial contribution of three-year-olds to the total CPE and then using a linear constant to calculate the actual number of three-year-old recruits. The actual estimates of recruitment and spawning stock biomass are presented in Appendix 4 and illustrated in Figure 5.

The parameters of the recruitment function were estimated by the logarithmic transformation technique presented by Ricker (1975). The following is the regression model used:

$$\ln (R/S) = \ln \alpha - \beta S$$

Estimated values for the parameters are: $\alpha = 1.409$ $\beta = 3.413 \times 10^{-7}$. The standard deviation of the error term v was calculated from the standard deviation of the regression residuals at 0.736.

The maximum age simulated was set at 15 years. This value was adequate since extremely few whitefish were found to be older than 14 years, even in the most lightly exploited stock sampled in this study.

The selection of a proper Δt and simulation run length is important for accurate simulations. A sufficiently small Δt will result in accurate numerical integrations. Also, the simulation must run long enough to produce an adequate estimate of the mean annual yield from the fluctuating population.

Table 4 illustrates the results of an analysis performed to determine an acceptable value for Δt (Manetsch and Park 1981). Several simulations were made with the controllable input values constant and removing the random recruitment factor. The time step was progressively shrunk with each simulation and the simulated yield converged to a "true" solution. An integration error of approximately 0.7% was associated with a Δt of 0.05. It was assumed that any integration error of less than 1% would be negligible.

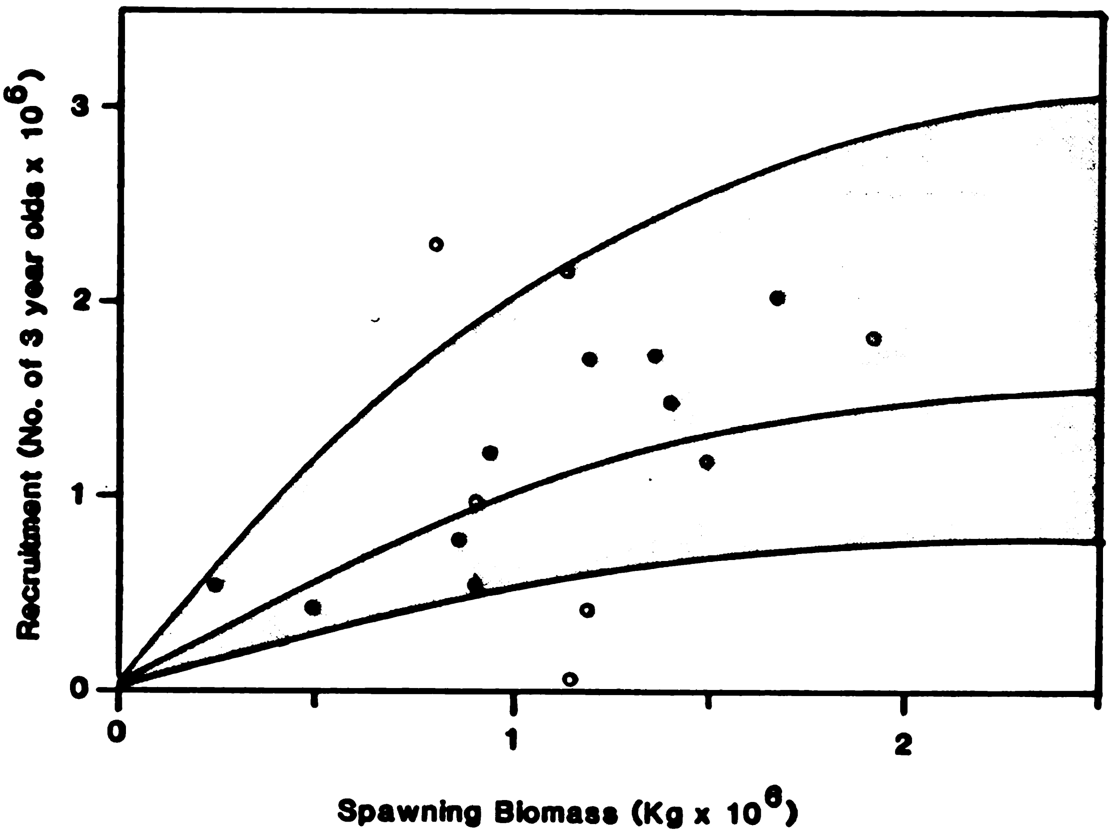


Figure 5. Stock-recruitment curve for lake whitefish in northern Lake Michigan. The shaded area represents ±1 standard deviation around the fitted line.

Table 4. Simulated yield values for different time steps. Controllable inputs set at $F_T^* = 0.654$, $F_G^* = 0.554$, MSL = 432 mm and m_G = 228 mm with no random recruitment factor ($v = 0$).

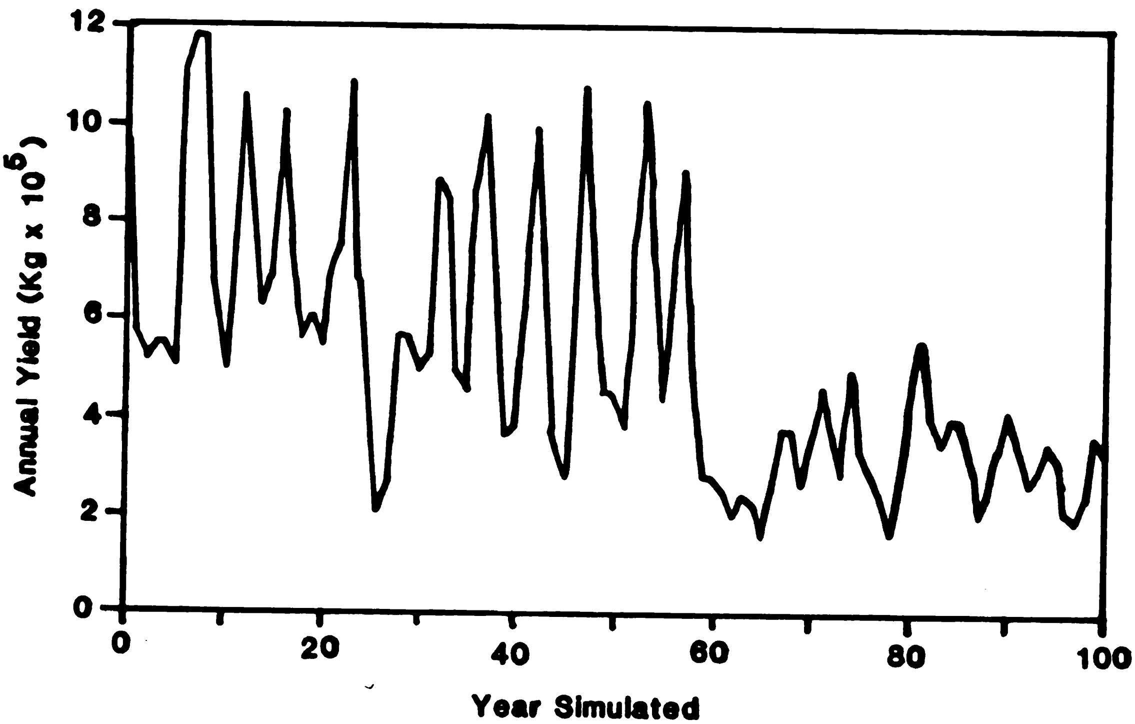
Δt	Yield
0.25 yrs	495,541 kilograms
0.10	482,272
0.05	477,914
0.01	474,953

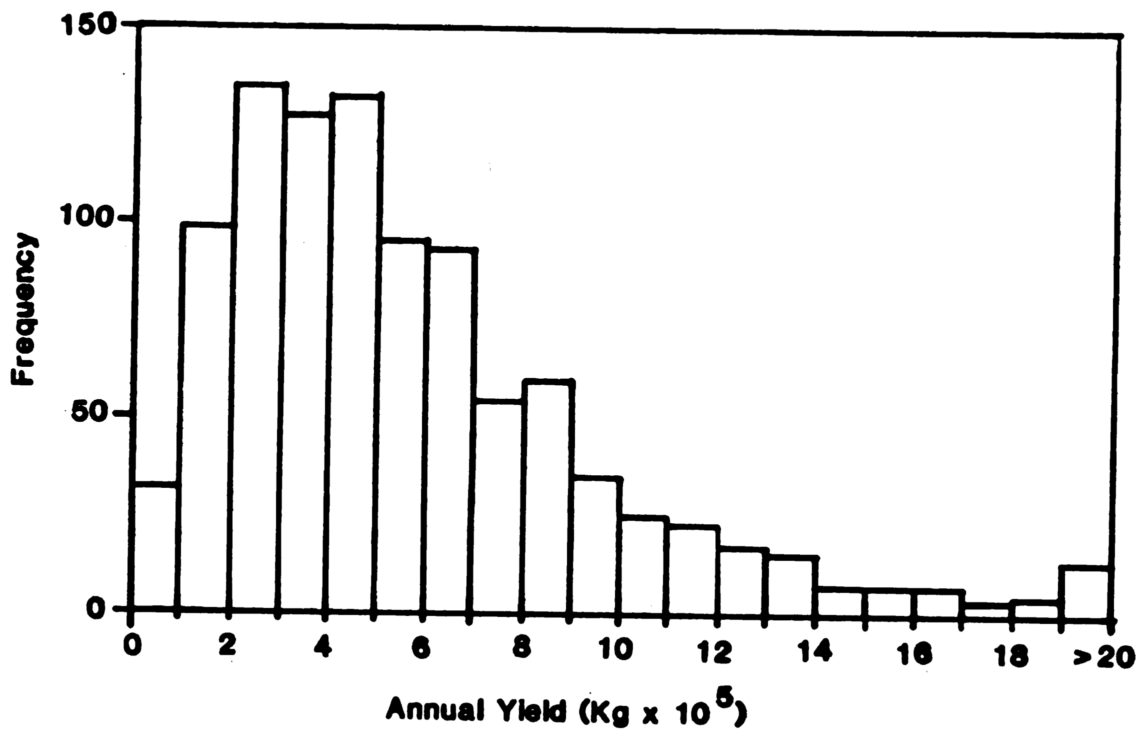
A similar technique was used to determine a suitable simulation run length. With the random recruitment factor operating, sets of five simulations were made at several different run lengths (Table 5). The standard deviation of yield from each set of runs decreased as the run length increased. A coefficient of variation (standard deviation of 5 runs/mean of 5 runs) of less than 2% was assumed to be acceptable. The run length of 1000 years meets this criterion and was used for further simulations.

Figure 6a is a time trace of the first one hundred years of annual yield (of a thousand year run) simulated under the present fishing mortality regimes ($F_T^* = 0.654$ and $F_G^* = 0.554$). The existence of relatively extended periods of low production, interpersed with periods of relatively high production, was characteristic of many of the simulations. The resulting histogram of annual yield frequency is presented in Figure 6b. The skewed distribution of yield was common to all the simulations and is probably a result of the log-normal stochastic recruitment factor.

Table 5. Means, standard deviations and coefficients of variation at five separate simulations made at four different run lengths. Controllable inputs set at $F_T^* = 0.654$, $F_G^* = 0.554$, MSL = 432 mm and $m_G = 228$ mm.

Run Length	Standard Deviation	C of V
100 years	33,414 kgs	0.0556
300	31,450	0.0543
600	20,564	0.0349
1000	8,189	0.0139





Figures 6a and 6b. Time trace of the first 100 years of annual yield in a 1000 year simulation (Fig. 6a) and the resulting histogram (Fig. 6b). Controllable inputs were $F_T^* = 0.654$, $F_G^* = 0.554$, MSL = 432 mm and m_G = 228 mm.

SIMULATION ANALYSIS

The future direction of the lake whitefish commercial fishery in northern Lake Michigan is uncertain at this time. The possibilities range from an exclusive trap net fishery to an exclusive gill net fishery. Because of this uncertainty, a scenario approach proved valuable in analyzing the possible forms the fishery may take. The simulations were organized into three separate scenarios:

Scenario #1 - Multigear fishery with gear-specific fishing mortality as controllable inputs.

Scenario #2 - Trap net fishery only with fishing mortality and minimum size limits as controllable inputs.

Scenario #3 - Gill net fishery only with fishing mortality and mesh size limitations as controllable inputs.

The general approach was to identify possible sets of controllable inputs which produce an optimum sustainable yield, OSY being defined as a large sustainable yield with a relatively low level of variability.

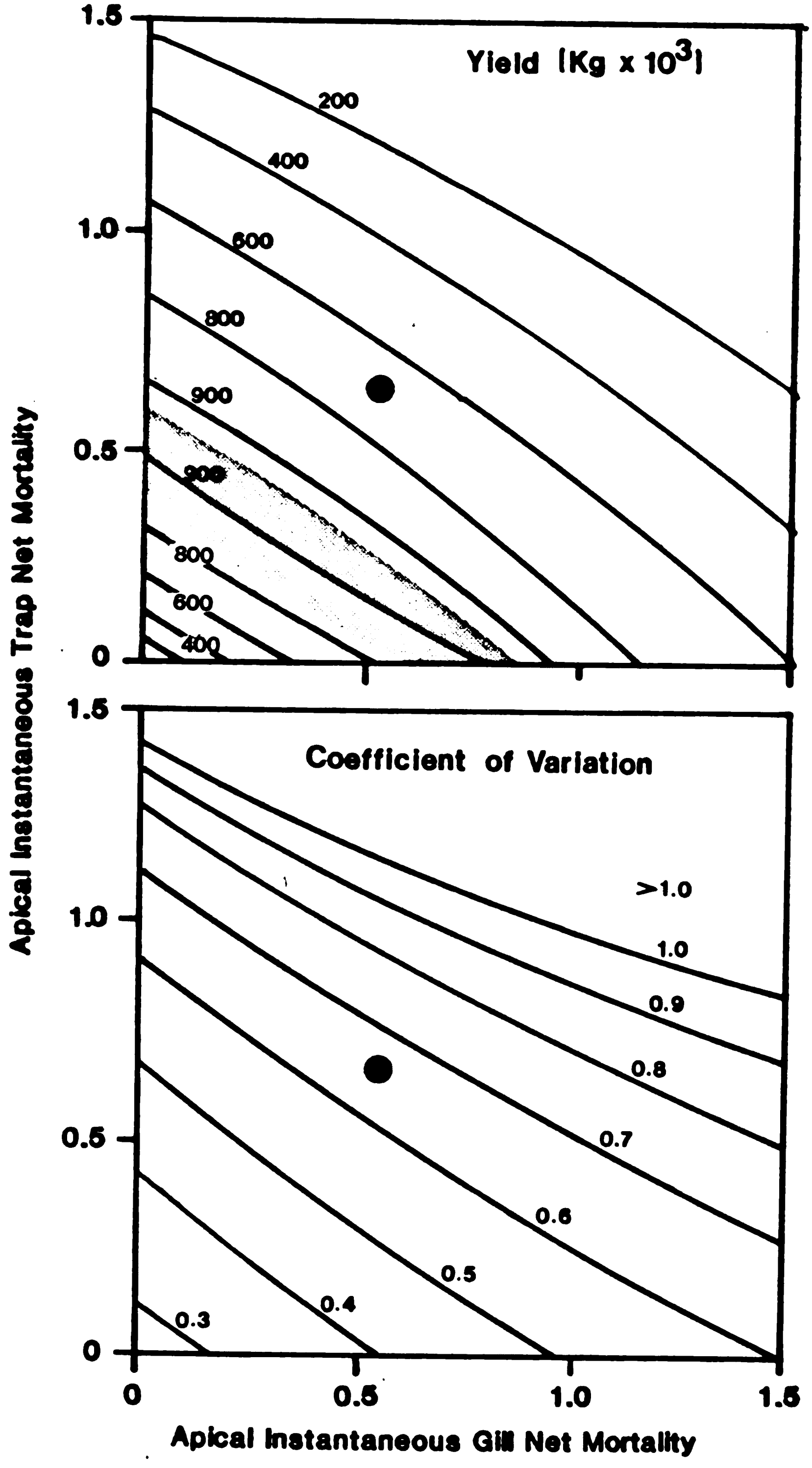
SCENARIO #1 - Multigear fishery with gear-specific fishing mortality rates as controllable inputs.

One of the key questions concerning the fishery in northern Lake Michigan is whether or not the present level of exploitation is excessive and leading to a collapse of the whitefish stocks. The simulations of the first scenario investigated the effects of the current level of trap and gill net mortality on the long term yield and stability of the population.

Several simulations were made at various combinations of apical trap and gill net fishing mortality rates (with the trap net minimum size limit and gill net mesh size set at their current values: 432 mm and 114 mm, respectively). Figure 7a is a graphical summary of these many simulation runs. Sustainable yields are presented as a contoured representation of a topological surface displaying isopleths of equal mean annual yield at various combinations of gear-specific apical fishing mortalities. The general shape of this yield contour diagram shows low yield at low levels of fishing mortality, increasing to a ridge of high yield at moderate fishing levels and then tapering back off to low yields at high fishing mortality rates.

The present status of the fishery is indicated in the figure by a black dot. The simulated mean annual yield of 700,000 kilograms is very close to the actual 1981 yield of 792,752 kilograms. This would indicate that the present high levels of yield can be sustained. However, the comparison of simulated yields with actual yields must be made with caution. The exact predictive power and relative accuracy of the model are unknown. A more valid comparison is one between simulated values. The relative position of the current fishery on the yield contour ridge indicates that higher sustainable yields are possible with a reduction of fishing effort - either trap or gill net mortality.

The variability in annual yield is represented in Figure 7b by contours of equal coefficients of variation at



Figures 7a and 7b. Isopleths of simulated mean annual yield (Fig. 7a) and coefficient of variation (Fig. 7b) for lake whitefish in northern Lake Michigan in a multi-gear fishery. Controllable inputs of MSL - 432 mm and m_G = 228 mm. Shaded area represents possible OSY's. Black dots represent the current state of the fishery.

different combinations of fishing mortality. As expected, the level of variability increases steadily as fishing mortality increases. The current fishery operates within an area of moderate variability; coefficient of variation approximately equal to 0.66.

Population age structure is a primary factor influencing the relative magnitude of annual yield variability. High coefficients of variation are associated with relatively narrow age compositions because of a greater dependence of spawning success on fewer age classes. The relative effects of weak year classes on the variability in recruitment are greater for populations with narrow age compositions. Broad age compositions produce less variability in recruitment because of the many age groups present. Figure 8 illustrates actual age compositions derived from samples of the commercial trap net catch for different stocks within the study area. The north shore population exhibits the narrowest age composition, a direct result of high fishing mortality (total annual mortality = 70.8%-Scheerer 1982). The lightly fished population near Leland has the broadest age composition (total annual mortality = 58.6%-Scheerer 1982). The Beaver Island sample exhibits an age structure intermediate to the surrounding areas (total annual mortality = 65.8%-Scheerer 1982). A reduction in the fishing effort exerted on the north shore stock would shift the age structure toward a broader composition and would eventually reduce the annual variability in yield.

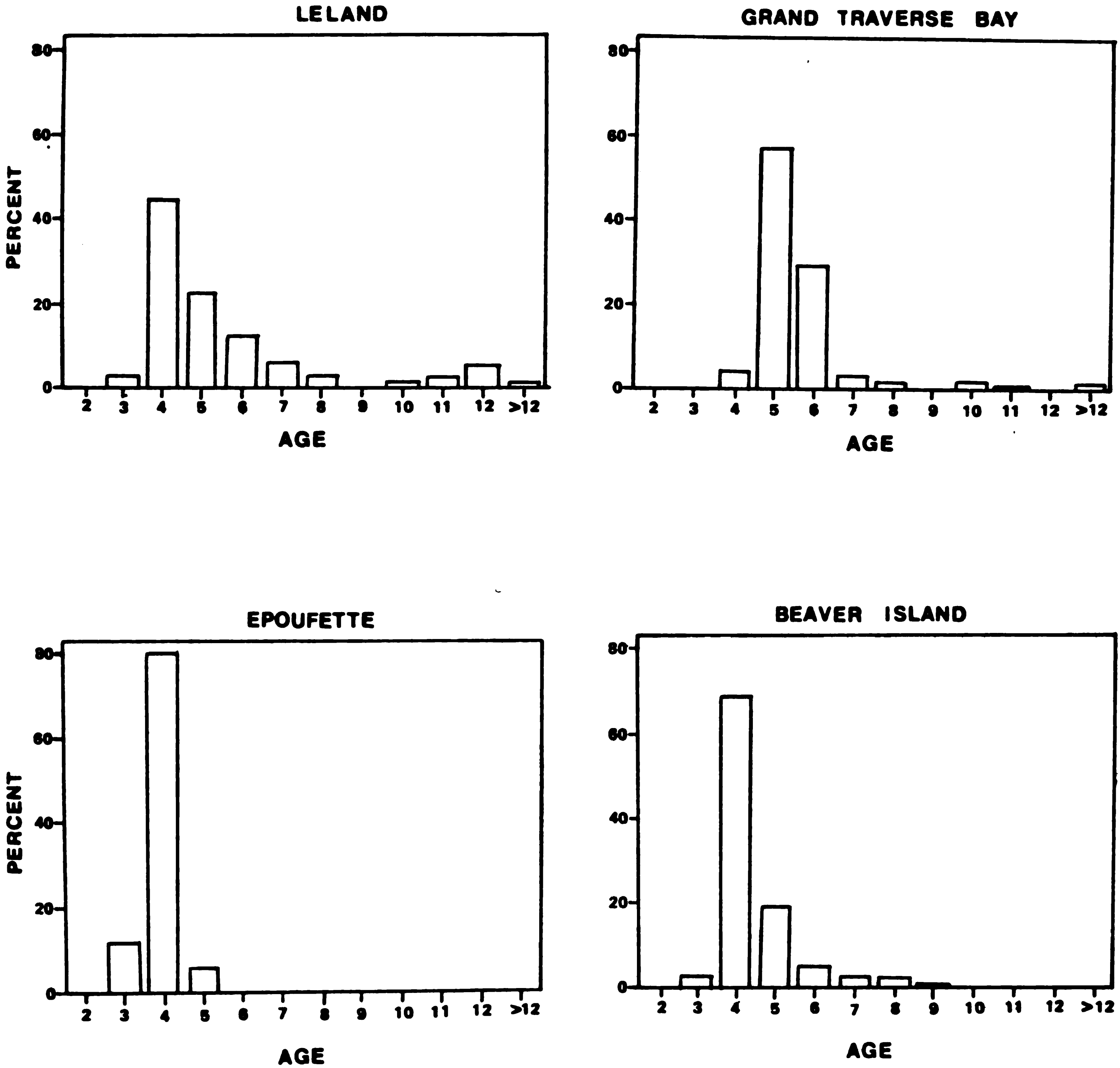
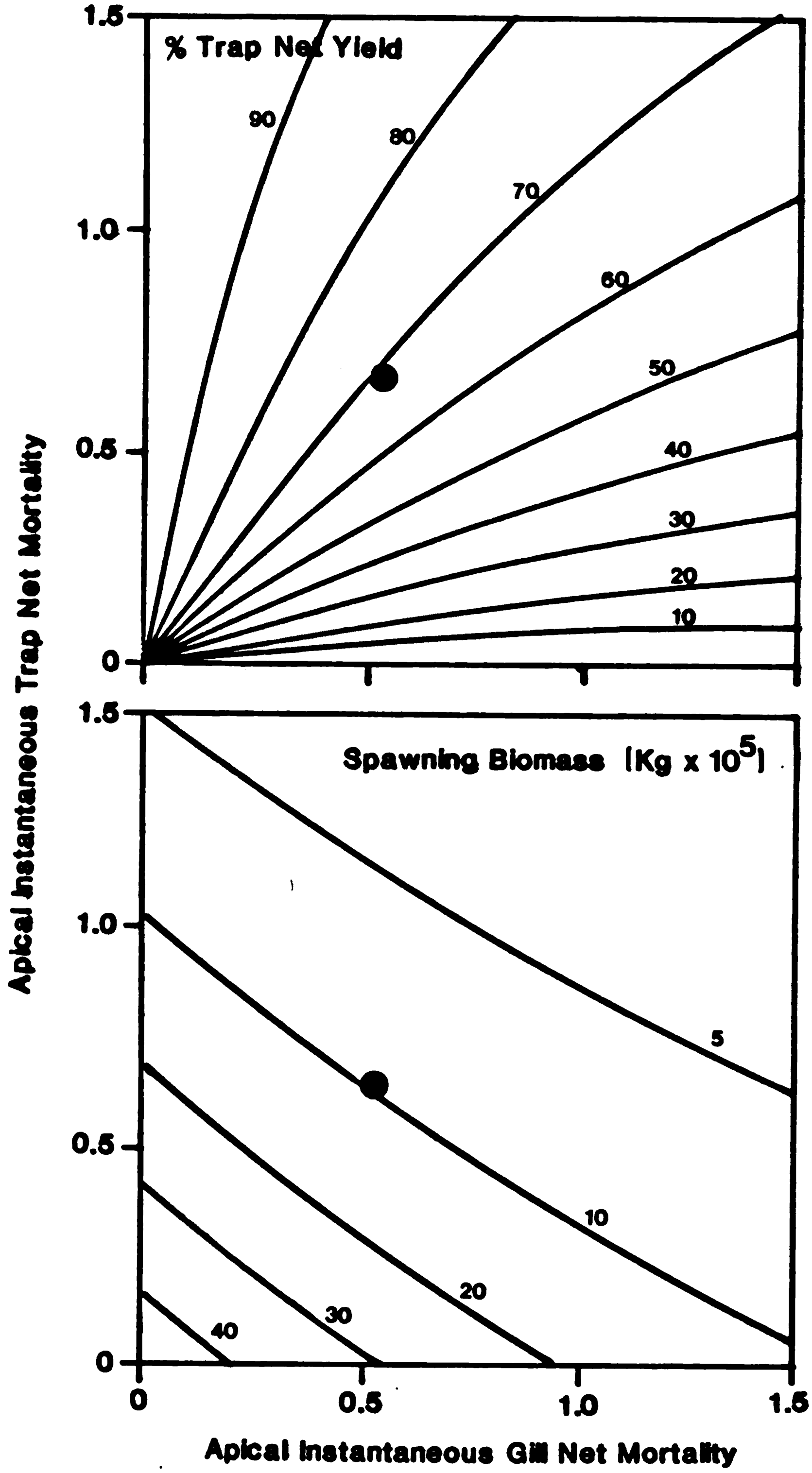


Figure 8. Age compositions of lake whitefish in northern Lake Michigan from commercial catch samples in the spring of 1981.

The total catch is broken down by gear types in Figure 9a. As expected, the general trend indicates a higher percentage of the total yield being harvested by trap nets at high trap net fishing mortalities and vice versa for gill net mortalities. Trap nets currently harvest the majority of the total whitefish catch (65% actual and 68% simulated). Equal allocation is represented in the figure by the 50% isopleth.

Isopleths of mean spawning biomass are illustrated in Figure 9b. The largest spawning biomasses are associated with the smallest fishing mortalities. The simulated mean spawning biomass of 1 million kilograms represented by the current status of the fishery agrees reasonably well with the actual 1980 biomass estimate of 1.4 million kilograms.

General areas of the parameter space can be identified which meet the requirements of OSY as previously defined. The shaded area of the lower left hand portion of the yield ridge in Figure 7a produces a relatively low level of variability (Figure 7b) and a high sustainable yield. If an equal allocation of harvest between gear types is desired, the intersection of this ridge and the 50% allocation isopleth produces the satisfactory combination of mortality rates. For example, an apical trap net mortality of 0.3 and an apical gill net mortality of 0.4 would produce an annual yield of 900,000 kilograms, a coefficient of variation of 0.45 and an equal allocation between gear types. To achieve these mortality rates, the trap net effort would



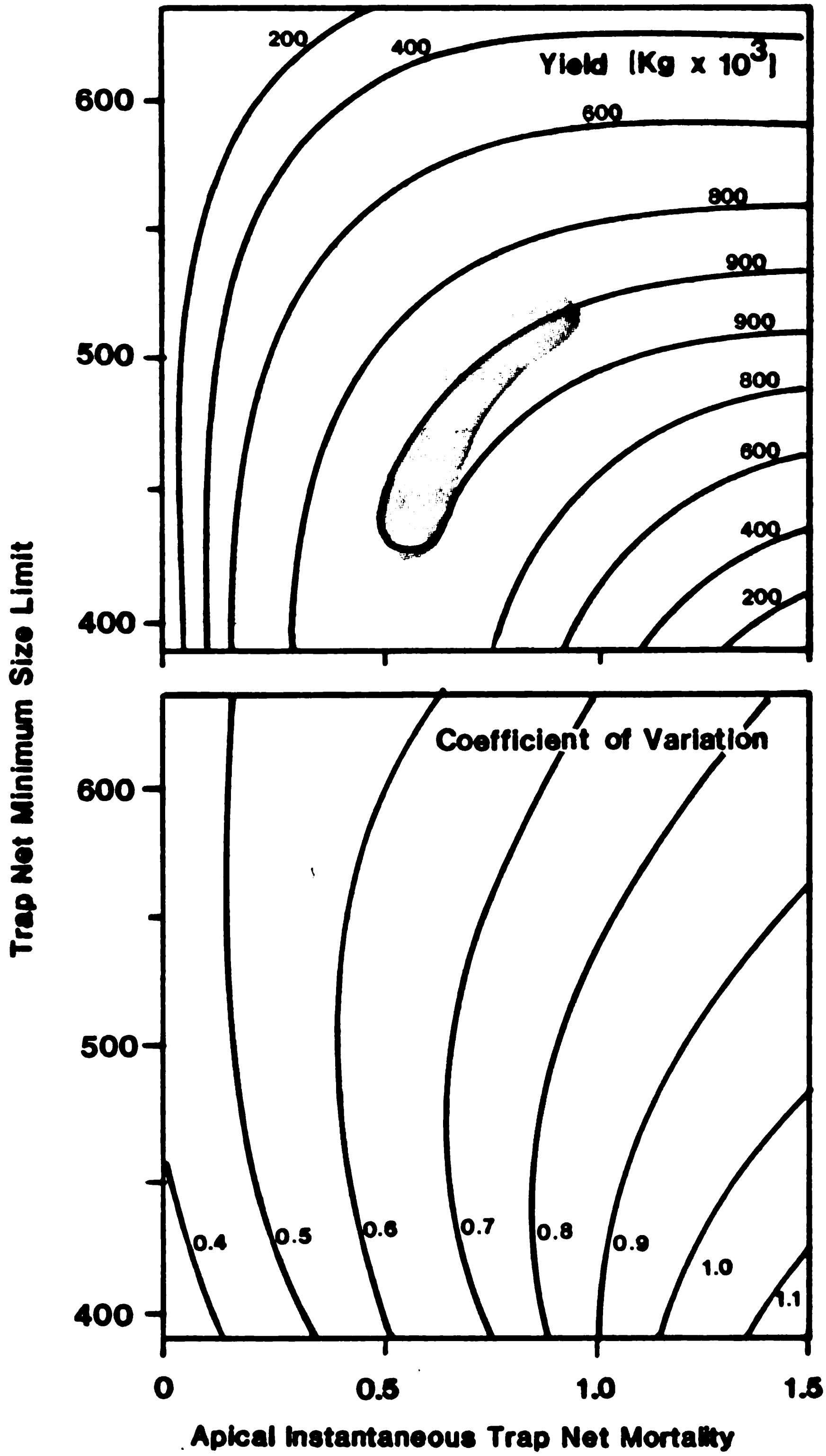
Figures 9a and 9b. Isopleths of percent trap net yield (Fig. 9a) and spawning biomass (Fig. 9b) of lake whitefish in northern Lake Michigan in a multi-gear fishery with MSL = 432 mm and m_G = 228 mm. Black dots represent the current state of the fishery (1981).

have to be reduced by 54 percent, and gill net effort by 28 percent from their 1981 levels (assuming a linear relationship between apical instantaneous fishing mortality and fishing effort). A reduction in effort of this magnitude would have obvious short term detrimental effects on the fishing industry. Although the current level of exploitation is somewhat less than optimally efficient, it is probably not exerting a catastrophic impact on the stock. Therefore, a gradual reduction in fishing effort may be the most desirable approach to take.

SCENARIO #2 - Trap net fishery only with fishing mortality rates and minimum size limits as controllable inputs.

The simulation analysis of this scenario identified the combinations of fishing mortality and trap net minimum size limits that produce OSY in an exclusive trap net fishery. The contour diagrams in Figures 10a and 10b represent graphical summaries of numerous simulations run with different sets of controllable inputs.

The first figure illustrates the isopleths of sustainable yields associated with the various combinations of trap net mortality and size limits. The diagram is directly analogous to a Beverton-Holt (1957) dynamic pool, yield isopleth diagram, except the absolute yield is plotted rather than yield per recruit. The optimal minimum size limit depends heavily on the level of fishing mortality. Considerably more fishing effort can be expended at a 500 mm minimum size limit than a 450 mm limit and still produce relatively large yields.



Figures 10a and 10b. Isopleths of simulated mean annual yield (Fig. 10a) and coefficient of variation (Fig. 10b) for lake whitefish in a hypothetical exclusive trap net fishery in northern Lake Michigan with MSL = 432 mm. Shaded area represents possible OSY's.

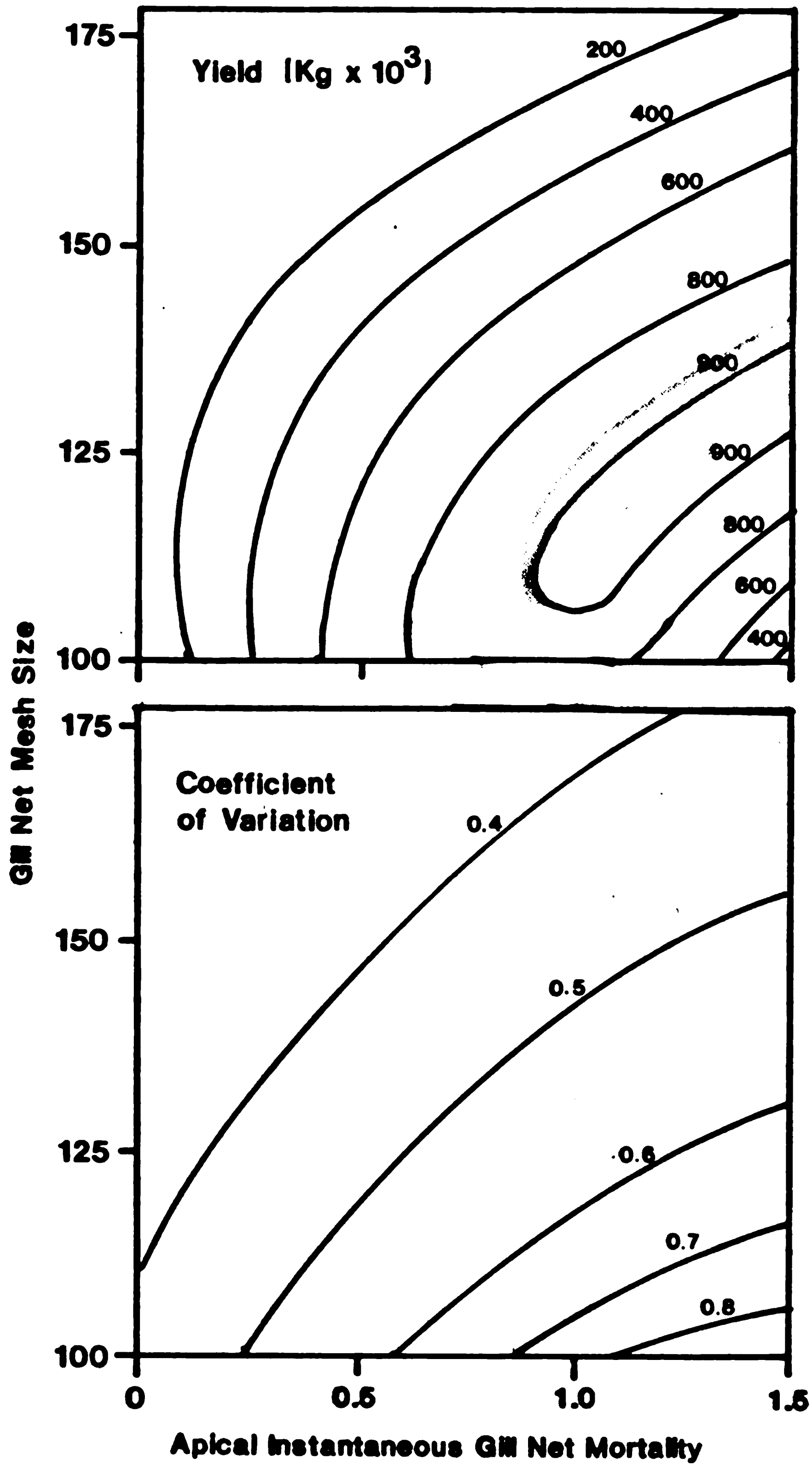
The coefficient of variation contour diagram is presented in the second figure. The variability in annual yield ranges from 0.4 at low fishing mortalities to 1.1 at high fishing mortalities. Minimum size limits also affect yield variability with the highest coefficient of variation being associated with the lowest minimum size limits.

The shaded area in the figures represent the possible combinations of trap net mortality and minimum size limits which produce OSY. If the fishery does move to an exclusive trap net fishery, it would be advisable to hold the trap net effort at the 1981 level. The current apical fishing mortality rate of 0.654 and minimum size limit of 432 mm would produce a yield of 900,000 kilograms. However, if an increse in trap net effort were to be unavoidable, a higher minimum size limit than the present 432 mm would be required to maintain a relatively high sustainable yield with moderately low variability.

<u>SCENARIO #3</u> - Gill net fishery only with fishing mortality and mesh size limitations as controllable inputs.

A third possible direction the fishery might take is one towards an exclusive gill net fishery. Management strategies include the regulation of fishing mortality and gill net mesh size. The simulation of this scenario investigates the effects of these two controllable inputs on sustainable yield and variance.

The yield contour diagram in Figure 11a is similar to the trap net diagram in Figure 10a with gill net mesh size



Figures 11 a and 11b. Isopleths of simulated mean annual yield (Fig. 11a) and coefficient of variation (Fig.11b) for lake whitefish in a hypothetical exclusive gill net fishery in northern Lake Michigan, with m_G = 228 mm. Shaded area represents possible OSY's.

used in place of trap net minimum size limit. Maximum yields occur at apical fishing mortalities of 0.8 to 1.5 and mesh sizes of 110 mm to 130 mm (stretched mesh). Considerably more fishing effort can be expended at a mesh size of 130 mm than a mesh size of 110 mm and still produce high yields.

Isopleths of the coefficients of variation associated with various combinations of controllable inputs are presented in Figure 11b. Variability increases as fishing mortality increases and mesh sizes decrease. The highest variability occurs at the highest fishing mortalities and the smallest mesh sizes.

The shaded areas in the figures represent possible sets of controllable inputs which result is OSY. The 1981 apical gill net fishing mortality of 0.554 and mesh size of 114 mm would produce a yield of 750,000 kilograms if the present trap net fishery were entirely eliminated. The stock could also absorb a considerable increase in gill net effort and still maintain relatively high yields.

OTHER MODEL APPLICATIONS

In addition to the scenarios presented above, there are other interesting combinations of the controllable inputs which can be simulated. For example, the optimal trap net minimum size limit in a multigear fishery is another pertinent management question. Figure 12 illustrates the sustainable yields produced from various trap net minimum size limits with gear-specific fishing mortalities held at 1981 levels.

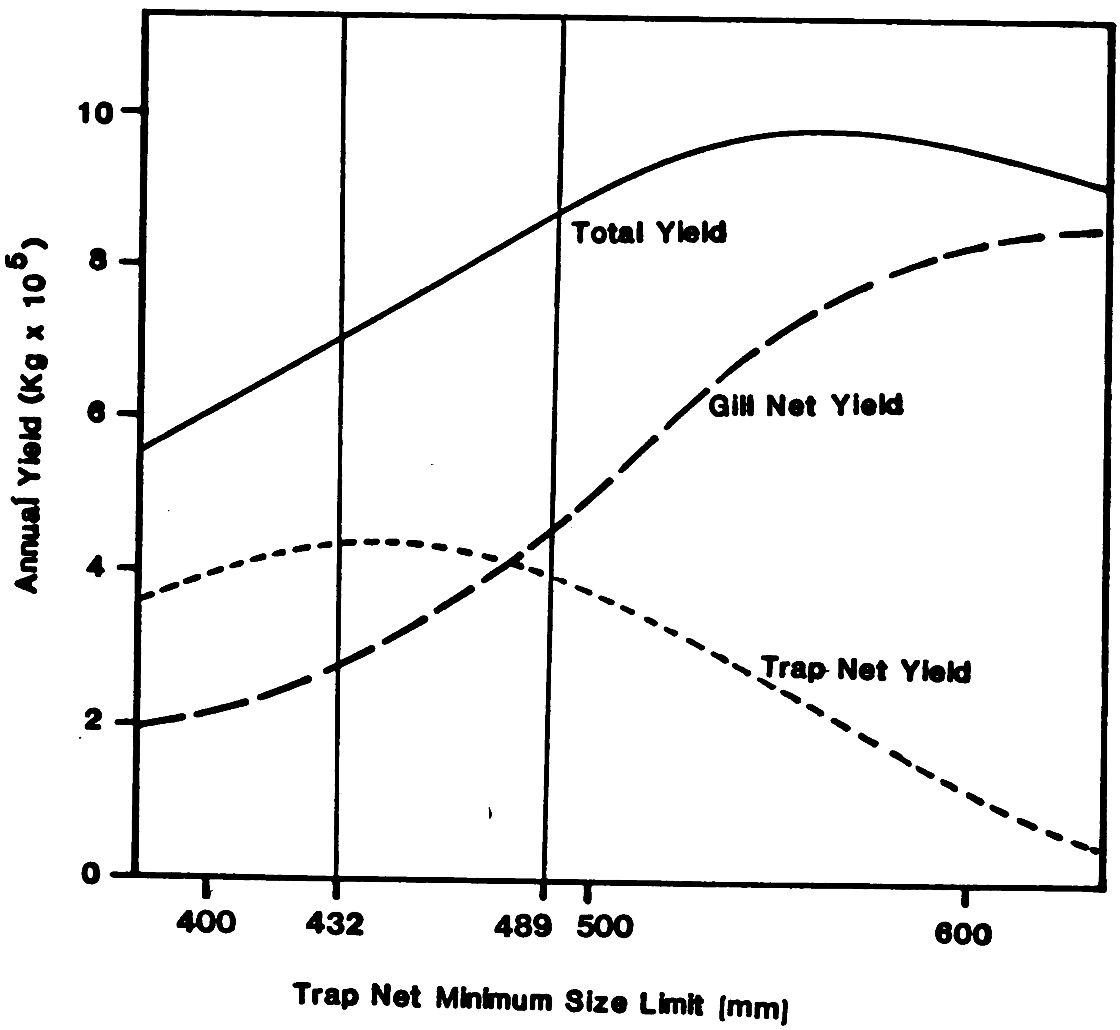


Figure 12. Simulated mean annual yield at different trap net minimum size limits for lake whitefish in a multi-gear fishery in northern Lake Michigan. Other controllable inputs set at their 1981 values: $F_T^* = 0.654$, $F_G^* = 0.554$ and $m_G = 228$ mm.

The maximum sustainable yield occurs at a size limit of 550 mm and the harvest would be done primarily by gill nets. A size limit of 480 mm produces a yield allocated equally to each gear type, but has a slightly lower sustainable yield.

There is currently discussion within the regulatory agencies to raise the trap net minimum size limit to 489 mm from the current 432 mm. Although the total sustainable yield would rise slightly, the major effect would be a shift from a harvest dominated by trap nets (68%) to a harvest dominated by gill nets (53%). The 114 mm stretched mesh gill nets would be harvesting cohorts considerably earlier than would trap nets.

Another interesting aspect of a multigear fishery concerns the inherent stability characteristics of each gear type. Does one gear produce a more stable yield than the other? Figure 13 illustrates the coefficients of variation at different levels of simulated sustainable yield for each gear type when fished exclusively. A trap net has a slightly lower associated level of variability than a gill net does for any given yield. This is due primarily to the inherent selectivity of each gear. The trap net harvests fish over a much broader range of fish lengths than does a single-sized mesh gill net. However, if mesh size limitations are in the form of minimum size mesh restrictions and fishermen are not required to use a single mesh size this may not be the case. Knowledgeable gill net fishermen are

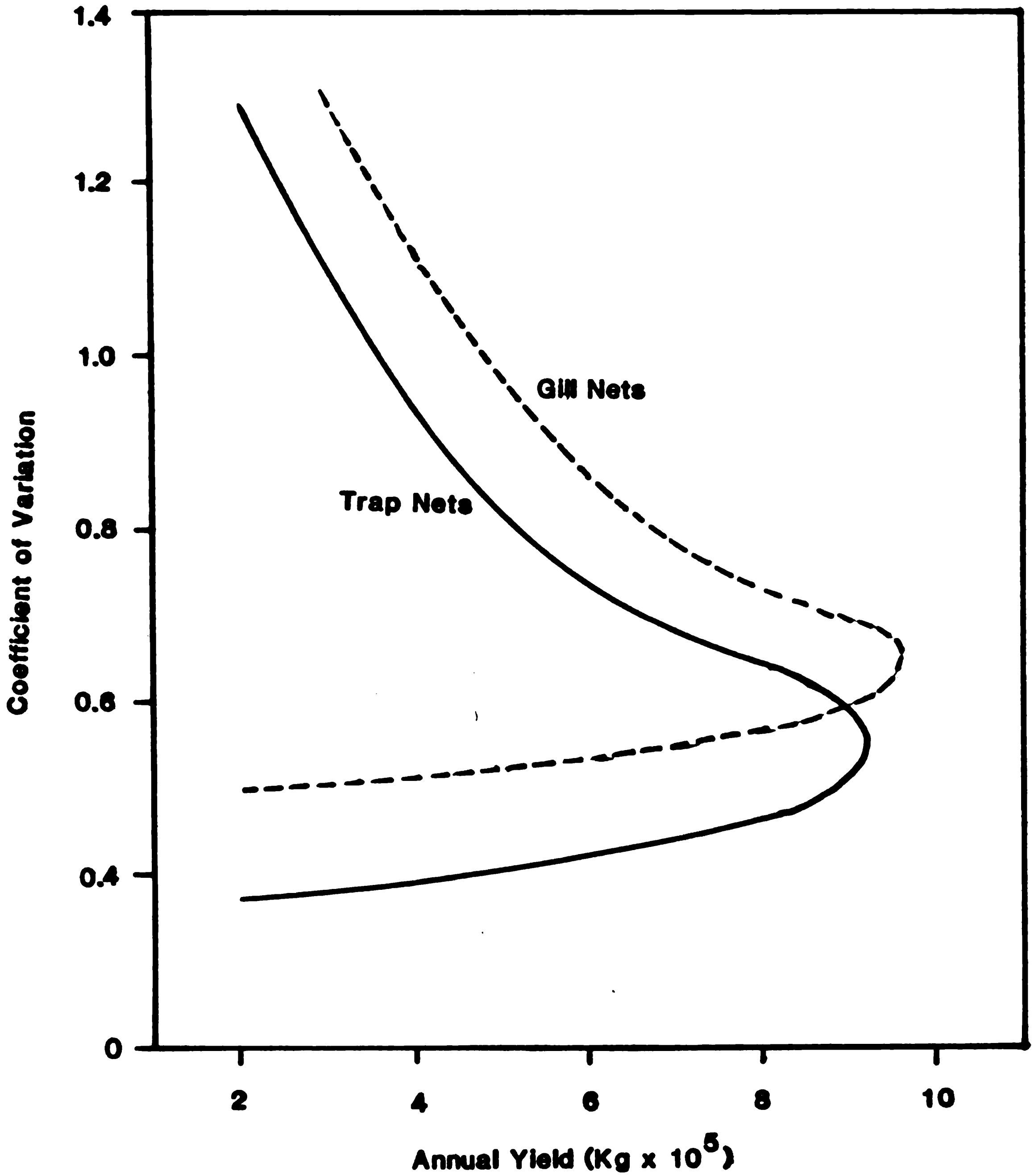


Figure 13. Simulated coefficients of variation in yield of lake whitefish in northern Lake Michigan at different mean annual yields when each gear is fished exclusively. Controllable inputs of MSL = 432 mm and m_G = 228 mm.

able to "track" strong cohorts by using nets of different mesh size as the year class grows which reduces the overall variability. But with a single-size mesh restriction, trap nets do produce a slightly more stable yield than do gill nets.

MODEL LIMITATIONS

While a simulation analysis is a valuable approach to this type of problem, certain inherent limitations must be kept in mind when interpreting the results. One potential weakness involves the possible inaccurate estimates of sensitive key parameters which can significantly distort the model behavior. Table 6 contains the results of a sensitivity analysis of the model parameters. Each parameter value was increased 10% and then decreased 10%, holding the others constant and noting the deviation in simulated yield for each change (with the random recruitment factor not operating). This identified the relative sensitivity of each parameter. The length-weight relationship (b) was the most sensitive. In fact, the model output was not stable (fluctuated chaotically) for either a 10% increase or decrease in this parameter. It enters the model in an exponential fashion, which greatly magnifies a 10% change in its value. Fortunately, the length-weight parameters were among the most accurately estimated, being derived from a sample of 1577 fish.

The recruitment function parameters were also identified as being relatively sensitive. Unfortunately, the

Table 6. Results of the sensitivity analysis performed on the model parameters. The deviation in simulated yield which resulted from a ±10% change in each parameter is listed.

Parameter	Deviation from a -10% change	Deviation from a +10% change
a	-0.0936	+0.0847
b	-	-
α	-0.0936	+0.0847
β	+0.1111	-0.0909
L_∞	-0.2298	+0.3007
K	-0.0802	+0.1613
A	-0.0074	+0.0060
B	-0.1027	+0.0086
M	+0.1105	-0.1051
C_1	-0.0020	+0.0015
C_2	+0.0248	-0.0571
μ_G	+0.0013	-0.0038
σ_G	+0.0055	-0.0060
C_G	-0.0258	+0.0250

Deviation = [(simulated yield from +10% change in parameter value) - (simulated yield from no change in parameter value)]/(simulated yield from no change in parameter value) accuracy of these two important parameters is unknown. There are several problems associated with the estimation procedures (Appendix 3) used to calculate spawning biomass and recruitment. Most serious is the possibility that CPE may not be directly proportional to stock size (either spawning biomass or number of three-year-olds). Trap net effort is measured by kilograms per lift, but soak time (number of nights out) is not considered. If fishermen tend to leave their nets out longer when there are fewer fish present, the reported CPE would overestimate fish abundance. Improvements in the gear or the fishermen's expertise over time would also complicate the relationship. A problem specifically related to the recruitment estimation procedure is that the relationship may be complicated by density dependent body growth. The first significantly vulnerable age group is the three-year-olds. Therefore, the rate of growth may be important in determining the portion of the cohort entering the fishery. For example, a large cohort might be underrepresented because of slower body growth. The spawning biomass and recruitment estimates are, admittedly, the least accurate of all the data used to estimate the parameters.

Another problem with the stock-recruitment relationship is that the behavior of the function at high stock levels comes entirely from the extrapolation of a statistically fitted line. However, the fit appears to be biologically reasonable for this population. The curve is consistent with the observation that the recent large recruitments of 2 million three-year-olds are probably near the maximum possible for this stock.

A serious limitation of the simulation model is that no mechanism for density-dependent body growth was incorporated. Several authors have reported relatively slower rates of growth associated with higher densities of lake whitefish. Healey (1979), noted this phenomonon in several northern Canadian lakes and Jensen (1982) inferred, by a mathematical analysis, the importance of density-dependent body growth in the population regulation in lake whitefish. The potential effects of density-dependent body growth could be very important if the north shore population biomass has the real capability of increasing to the simulated 4 million kilograms with very light fishing pressure (Figure 9b). The model behavior would be affected at high stock densities (extreme lower left-hand corners of Figures 7a, 7b, 9a and 9b). However, the extent to which density-dependent growth is important to the whitefish population in northern Lake Michigan is not known.

Even with these possible inherent weaknesses, it is felt that the model is biologically sound and realistically simulates the population dynamics of this stock over relatively wide ranges of population size.

CONCLUSION

The whitefish stock in northern Lake Michigan is probably not in imminent danger of collapse, but is operating at a point somewhat less than optimal efficiency. Although a reduction in fishing effort would eventually produce a larger yield, the short term effects would be detrimental to the fishing industry. An abrupt reduction in fishing effort would be undesirable since the present fishery is capable of producing large, sustainable annual yields of 700,000 kilograms.

APPENDICES

Appendix 1. Glossary of variable names used in the text.

a - length-weight parameter

A - length-girth parameter

α - stock-recruitment parameter

b - length-weight parameter

B - length-girth parameter

β - stock-recruitment parameter

C_1 - trap net selectivity constant

C_2 - trap net selectivity constant

CV - coefficient of variation of yield

$F_{G,i}(t)$ - instantaneous gill net fishing mortality rate operating on cohort i at time t

$F_{T,i}(t)$ - instantaneous trap net fishing mortality rate operating on cohort i at time t

F_G^* - apical instantaneous gill net fishing mortality rate

F_T^* - apical instantaneous trap net fishing mortality rate

$g_i(t)$ - girth of fish in cohort i at time t

i - cohort integer age

I_{MAX} - maximum age attained

K - von Bertalanffy growth parameter

$l_i(t)$ - length of fish in cohort i at time t

l_M - length at maturity

L_∞ - von Bertalanffy asymptotic length parameter

m_G - gill net mesh perimeter (equal to 2x stretched mesh measurement)

m_T - trap net mesh perimeter (equal to 2x stretched mesh measurement)

$M_i(t)$	- instantaneous natural mortality rate operating on cohort i at time t
MSL	- trap net minimum size limit
μ_G	- gill net selectivity parameter - mean
n_{MAX}	- simulation run length
$N_i(t)$	- number of fish in cohort i at time t
R	- recruitment
$RE_{G,i}(t)$	- relative efficiency of gill nets on cohort i at time t
$RE_{T,i}(t)$	- relative efficiency of trap nets on cohort i at time t
S	- spawning biomass
σ_G	- gill net selectivity curve parameter - standard deviation
t_0	- von Bertalanffy growth parameter
t_R	- time at recruitment
v	- random recruitment factor
$w_i(t)$	- weight of fish in cohort i at time t
$Y_{G,i}(t)$	- gill net yield of cohort i at time t
Y_n	- yield in year n
$Y_{POP}(t)$	- total population yield at time t
$Y_{T,i}(t)$	- trap net yield of cohort i at time t
$\overline{Y}$	- mean annual yield

Appendix 2. Fortran program of lake whitefish model.

```
C******** NORTHERN LAKE MICHIGAN WHITEFISH POPULATION MODEL ************
C
      PROGRAM WMOD(INPUT,OUTPUT)
      REAL LINF,K,LGR,MSL,MESHTN,MESHGN,MM
      REAL POP(0:15),LEN(0:15),YLDGN(0:15),YLDTN(0:15),FTN(0:15),FGN(0:1
     +5),M(0:15),NMVAL(41),DYTDT(0:15),DYGDT(0:15),DNDT(0:15),EPOP(0:15)
     +,EDYTDT(0:15),EDYGDT(0:15),EDNDT(0:15)
C
C         TABLE LOOK-UP FUNCTION VALUES
C
      DATA NMVAL /-3.500,-1.960,-1.645,-1.439,-1.281,-1.150,-1.037,-.925
     +,-.841,-.755,-.674,-.598,-.524,-.454,-.386,-.312,-.253,
     +-.189,-.126,-.056,0.0,.056,.126,.189,.253,.312,.386,.454,.524,.598
     +,.674,.755,.841,.925,1.037,1.150,1.281,1.439,1.645,1.960
     +,3.500/
C
C         CONTROLLABLE INPUTS
C
      MSL=431.8
      APFTN=0.654
      APFGN=0.554
      MESHTN=114.3
      MESHGN=114.3
C
C         PARAMETER VALUES
C
      A=4.24 E -9
      B=3.12
      ALPHA=1.409
      BETA=3.413 E -7
      SDVT=0.736
      LINF=713.8
      K=0.254
      AG=-32.98
      BG=0.5777
      LGR=381.0
      MM=0.368
      TNN=25.43
      TNK=0.9879
      GNMU=0.2303
      GNSD=0.1184
      GNK=0.3736
      KNORM=40
      DIFFNR=0.025
      SMALLN=0.0
C
C         SIMULATION RUN LENGTH,DELTA-T AND BUILD-UP PERIOD VALUES
C
      NBLDUP=20
```

```
      NYRS=1000
      NYITT=NYRS-1
      NYRSPB=NYRS-NBLDUP
      DT=0.05
      IDT=INT(1./DT+0.00001)
      CALL RANSET(TIME())
      PTN=MESHTN*2.00
      PGN=MESHGN*2.00
      PRINT 901,'1','GILLNET MESH SIZE',MESHGN
      PRINT 901,' ','TRAPNET MESH SIZE',MESHTN
      PRINT 905,' ','GILLNET FISHING MORTALITY (APICAL) ',APFGN
      PRINT 905,' ','TRAPNET FISHING MORTALITY (APICAL)',APFTN
      PRINT 901,' ','TRAPNET MINIMUM SIZE LIMIT',MSL
      PRINT 902,'0','YEAR','YIELD','SPAWNING STOCK','RECRUITMENT','TRAPN
     +ET YIELD','GILLNET YIELD'
C
C         INITIALIZE STATE VARIABLES
C
      DO 11 IN=0,15
      POP(IN)=0.0
      YLDTN(IN)=0.0
      YLDGN(IN)=0.0
11    CONTINUE
      POP(0)=1000000.
      POP(1)=1000000.
      POP(2)=1000000.
      POP(3)=400000.
      POP(4)=1272535.
      POP(5)=365906.
      POP(6)=26632.
      POP(7)=3326.
C
C          INITIALIZE RATE VARIABLES
C
      T=0.0
      DO 22 IP=0,15
      AGE=IP+T
      LEN(IP)=LINF*(1.00-EXP(-K*AGE))
      GIRTH=AG+BG*LEN(IP)
      IF(GIRTH.LE.0.0)THEN
      GIRTH=0.0001
      ELSE
      ENDIF
      GPRTN=GIRTH/PTN
      GPRGN=GIRTH/PGN
      PETN=GPRTN**TNN/(TNK**TNN+GPRTN**TNN)
      PEGN=GNK/(2.506628*GNSD*GPRGN)*EXP(-(LOG(GPRGN)-GNMU)**2/(2.0*GNSD
     +**2))
      FTN(IP)=APFTN*PETN
      FGN(IP)=APFGN*PEGN
      IF(LEN(IP).LT.LGR)THEN
```

```
      M(IP)=0.0
      FTN(IP)=0.0
      FGN(IP)=0.0
      ELSE
      M(IP)=MM
      ENDIF
      IF(LEN(IP).LT.MSL)THEN
      FTN(IP)=0.0
      ELSE
      ENDIF
      DYTDT(IP)=FTN(IP)*POP(IP)*A*LEN(IP)**B
      DYGDT(IP)=FGN(IP)*POP(IP)*A*LEN(IP)**B
      DNDT(IP)=-(FTN(IP)+FGN(IP)+M(IP))*POP(IP)
22    CONTINUE
      STYLD=0.0
      SUMSQY=0.0
      STNY=0.0
      SSQTN=0.0
      SGNY=0.0
      SSQGN=0.0
      SSB=0.0
      SSQSB=0.0
      SR=0.0
      SSQR=0.0
C        START YEARLY ITERATIONS
C
      DO 300 N=0,NYITT
C
C        START WITHIN YEAR ITERATIONS
C
      DO 200 J=1,IDT
      T=T+DT
C
C         START CALCULATIONS FOR EACH COHORT
C
      DO 100 I=3,15
C
C         CALCULATE LENGTHS AND MORTALITY RATES OF COHORT
C
      AGE=I+(T-N)
      LEN(I)=LINF*(1.00-EXP(-K*AGE))
      GIRTH=AG+BG*LEN(I)
      IF(GIRTH.LE.0.0)THEN
      GIRTH=0.0001
      ELSE
      ENDIF
      GPRTN=GIRTH/PTN
      GPRGN=GIRTH/PGN
      PETN=GPRTN**TNN/(TNK**TNN+GPRTN**TNN)
      PEGN=GNK/(2.506628*GNS0*GPRGN)*EXP(-(LOG(GPRGN)-GNMU)**2/(2.0*GNS0
```

```
     +**2))
      FTN(I)=APFTN*PETN
      FGN(I)=APFGN*PEGN
      IF(LEN(I).LT.LGR)THEN
      M(I)=0.0
      FTN(I)=0.0
      FGN(I)=0.0
      ELSE
      M(I)=MM
      ENDIF
      IF(LEN(I).LT.MSL)THEN
      FTN(I)=0.0
      ELSE
      ENDIF
C
C        INTEGRATE YIELD AND POPULATION FUNCTIONS
C
      EPOP(I)=POP(I)+DT*DNDT(I)
      EDNDT(I)=-(FTN(I)+FGN(I)+M(I))*EPOP(I)
      POP(I)=POP(I)+DT*(EDNDT(I)+DNDT(I))/2.00
      EDYTDT(I)=FTN(I)*POP(I)*A*LEN(I)**B
      YLDTN(I)=YLDTN(I)+DT*(EDYTDT(I)+DYTDT(I))/2.00
      EDYGDT(I)=FGN(I)*POP(I)*A*LEN(I)**B
      YLDGN(I)=YLDGN(I)+DT*(EDYGDT(I)+DYGDT(I))/2.00
      DYTDT(I)=FTN(I)*POP(I)*A*LEN(I)**B
      DYGDT(I)=FGN(I)*POP(I)*A*LEN(I)**B
      DNDT(I)=-(FTN(I)+FGN(I)+M(I))*POP(I)
100   CONTINUE
200   CONTINUE
C
C        CALCULATE SPAWNING BIOMASS
C
      SPBIOM=0.0
      DO 52 IB=0,15
      IF(LEN(IB).GE.431.8)THEN
      SPBIOM=SPBIOM+POP(IB)*A*LEN(IB)**B
      ELSE
      ENDIF
52    CONTINUE
C
C        GENERATE A RANDOM NUMBER NORMALLY DISTRIBUTED WITH MEAN=0.0 AND
C        STANDARD DEVIATION = SDVT
C
      UNRAN=RANF()
      RAN=TABLIE(NMVAL,SMALLN,DIFFNR,KNORM,UNRAN)
      VT=RAN*SDVT
C
C        GENERATE RECRUITMENT
C
```

```
      RECR=ALPHA*SPBIOM*EXP(-BETA*SPBIOM+VT)
C
C        CALCULATE ANNUAL YIELD STATISTICS
C
      TYLDGN=0.0
      TYLDTN=0.0
      TYLD=0.0
      DO 54 IA=0,15
      TYLDGN=TYLDGN+YLDGN(IA)
      TYLDTN=TYLDTN+YLDTN(IA)
54    CONTINUE
      TYLD=TYLDGN+TYLDTN
      IF(N.GE.NBLDUP)THEN
      STYLD=STYLD+TYLD
      SUMSQY=SUMSQY+TYLD**2
      SSB=SSB+SPBIOM
      SSQSB=SSQSB+SPBIOM**2
      SR=SR+RECR
      SSQR=SSQR+RECR**2
      STNY=STNY+TYLDTN
      SSQTN=SSQTN+TYLDTN**2
      SGNY=SGNY+TYLDGN
      SSQGN=SSQGN+TYLDGN**2
      ELSE
      ENDIF
C
C        AN ANNUAL SUMMARY IS PRINTED
C
      PRINT 903,N,TYLD,SPBIOM,RECR,TYLDTN,TYLDGN
C
C        UPDATE STATE AND RATE VARIABLES TO NEXT AGE GROUP
C
      DO 55 JI=15,1,-1
      POP(JI)=POP(JI-1)
      YLDTN(JI)=0.0
      YLDGN(JI)=0.0
      DYTDT(JI)=DYTDT(JI-1)
      DYGDT(JI)=DYGDT(JI-1)
      DNDT(JI)=DNDT(JI-1)
55    CONTINUE
      POP(0)=RECR
      YLDTN(0)=0.0
      YLDGN(0)=0.0
      DYTDT(0)=0.0
      DYGDT(0)=0.0
      DNDT(0)=0.0
300   CONTINUE
C
C        CALCULATE DESCRIPTIVE STATISTICS OF ANNUAL YIELDS
```

```
C
      AVEYLD=STYLD/NYRSPB
      SDYLD=SQRT((SUMSQY-STYLD**2/NYRSPB)/(NYRSPB-1))
      CVYLD=SDYLD/AVEYLD
      PRINT*
      PRINT*,'SIMULATION SUMMARY FOR YEARS PAST THE BUILD-UP PERIOD'
      PRINT 904,'0','AVERAGE ANNUAL YIELD',AVEYLD
      AVR=SR/NYRSPB
      SDR=SQRT((SSQR-SR**2/NYRSPB)/(NYRSPB-1))
      AVSB=SSB/NYRSPB
      SDSB=SQRT((SSQSB-SSB**2/NYRSPB)/(NYRSPB-1))
      AVTNY=STNY/NYRSPB
      SDTNY=SQRT((SSQTN-STNY**2/NYRSPB)/(NYRSPB-1))
      AVGNY=SGNY/NYRSPB
      SDGNY=SQRT((SSQGN-SGNY**2/NYRSPB)/(NYRSPB-1))
      PRINT 904,' ','STANDARD DEVIATION  ',SDYLD
      PRINT 906,' ','COEFFICIENT OF VARIATION',CVYLD
      PRINT 904,'0','AVERAGE TRAPNET YIELD',AVTNY
      PRINT 904,' ','STANDARD DEVIATION   ',SDTNY
      PRINT 904,'0','AVERAGE GILLNET YIELD',AVGNY
      PRINT 904,' ','STANDARD DEVIATION',SDGNY
      PRINT 904,'0','AVE SPAWNING BIOMASS',AVSB
      PRINT 904,' ','STANDARD DEVIATION',SDSB
      PRINT 904,'0','AVE NUMBER OF RECRUITS',AVR
      PRINT 904,' ','STANDARD DEVIATION',SDR
901   FORMAT (A,T10,A,T56,F10.1)
902   FORMAT (A,T6,A,T20,A,T26,A,T44,A,T57,A,T72,A)
903   FORMAT (1X,I8,5F15.1)
904   FORMAT(A,A,T27,F15.1)
905   FORMAT(A,T10,A,T56,F10.3)
906   FORMAT(A,A,T27,F15.3)
      END
      FUNCTION TABLIE(VAL,SMALL,DIFF,K,DUMMY)
C
C        TABLE LOOK-UP FUNCTION
C
      DIMENSION VAL(1)
      DUM=AMIN1(AMAX1(DUMMY-SMALL,0.0),FLOAT(K)*DIFF)
      I=1.0+DUM/DIFF
      IF(I.EQ.K+1)I=K
      TABLIE=(VAL(I+1)-VAL(I))*(DUM-FLOAT(I-1)*
     +DIFF)/DIFF+VAL(I)
      RETURN
      END
```

Appendix 3. Procedures used to calculate spawning biomass and recruitment of lake whitefish in northern Lake Michigan.

ESTIMATION OF SPAWNING BIOMASS

Assuming that the biomass of a population is directly proportional to the yield per unit effort by trap nets (Ricker 1975) the biomass at the time of spawning can be estimated by the following linear relationship:

$$S_z = C_S \; YPE_{T,z} \tag{A1}$$

where,

S_z = spawning biomass in year z

C_S = constant

$YPE_{T,z}$ = trap net yield per unit effort (kilograms per lift) in year z

The linear constant, C_S, was estimated from the biomass calculations made by Scheerer (1982) and catch/effort data from the Michigan Department of Natural Resources:

$$\begin{aligned} C_S &= S_{1980} \; / \; YPE_{T,1980} \\ &= 1{,}435{,}996 \text{ kgs} \; / \; (120.0 \text{ kgs/lift}) \\ &= 11967 \end{aligned} \tag{A2}$$

Actual biomass estimates for other years can then be calculated from historical YPE_T's using Equation A1. The estimates are presented in Appendix 4.

ESTIMATION OF RECRUITMENT

The same concept was used to calculate absolute recruitment. The number of three year old recruits is assumed to be directly proportional to the trap net yield per unit effort of three year old fish (YPE_3). The YPE_3's for past years were determined from the relative contributions of three year olds to the total YPE. These contributions were calculated from age compostitions from Brown (1968), Patriarche (1976), unpublished Michigan Department of Natural Resources reports and field data collected in this study. The specific steps used to determine the absolute recruitment are as follows:

1. The trap net yield per unit effort of three year olds is calculated for each year that age compositions are available:

$$YPE_{3,z} = P_z \; YPE_{T,z} \tag{A3}$$

where,

$YPE_{3,z}$ = trap net yield per unit effort of three year old fish in year z

P_z = percent by weight of three year old fish in the catch in year z

$YPE_{T,z}$ = total trap net yield per unit effort in year z

Before Equation A3 can be used, two preliminary steps are required. Because all of the age compositions are in terms of percent numbers of fish, they must be adjusted to percent weights of fish in order to calculate P_z. First, the mean weight of fish in each years catch is calculated:

$$\bar{w}_z = \sum_{i=0}^{I_{MAX}} w_i \, \theta_{i,z} \tag{A4}$$

where,

$\bar{w}_z$ = mean weight of fish in the catch in year z

w_i = weight at age i

$\theta_{i,z}$ = percent by number of age i fish in the catch of year z

Then, P_z can be calculated:

$$P_z = w_3 \, \theta_{3,z} \, / \, \bar{w}_z \tag{A5}$$

where,

w_3 = weight at age 3

$\theta_{3,z}$ = percent by number of age 3 fish in the catch of year z

Equation A3 can then be used.

2. The YPE's (kgs/lift) are transformed to CPE's (numbers/ lift):

$$CPE_{3,z} = YPE_{3,z} / w_3 \tag{A6}$$

where,

$CPE_{3,z}$ = catch per unit effort of three year olds in year z

3. The actual numbers of three year olds in the fall are calculated from Scheerer's fall 1980 population estimates:

$$N_{3f,z} = CPE_{3,z} \, C_R \tag{A7}$$

where,

$N_{3f,z}$ = number of three year olds in the fall of year z

C_R = constant

C_R is calcluated:

$$C_R = N_{3f,1980} / CPE_{3,1980} \tag{A8}$$

$$= 1,272,535 / 89.4$$

$$= 14234$$

4. The number of three year olds at the beginning of the year are calculated. First, the survival rate between the beginning of the year and the fall must be determined:

$$SR = \exp(-M(t_{441.8} - t_{381.0})) \tag{A9}$$

where,

SR = survival rate from the beginning of the year to the fall of the year

M = instantaneous natural mortality rate

$t_{441.8}$ = theoretical age when the cohort has a mean length of 441.8 mm (actual mean length of three year olds in the fall estimated by this study)

$t_{381.0}$ = theoretical age when the cohort has a mean length of 381.0 mm (length at the beginning of the year)

These theoretical times are calculated by rearranging the von Bertalanffy equation:

$$t = -\ln(1 - l(t)/L_{\infty}) / K \tag{A10}$$

Therefore,

$$t_{441.8} = 3.84$$

$$t_{381.0} = 3.00$$

5. The actual numbers of three year olds at the beginning of the year are calculated:

$$N_{3b,z} = N_{3f,z} / SR \tag{A11}$$

where,

$N_{3b,z}$ = number of three year old recruits at the beginning of the year (= R in the model)

Actual estimates of recruitment are presented in Appendix 4.

Appendix 4. Estimated spawning stock and recruitment for lake whitefish in northern Lake Michigan. Units are kilograms for spawning biomass and numbers of three-year-olds for recruitment.

Year of Spawning	Spawning Biomass	Recruitment
1956	257,000	550,000
1958	513,000	430,000
1963	919,000	586,000
1964	917,000	982,000
1965	850,000	764,000
1966	1,494,000	1,167,000
1967	1,121,000	2,212,000
1968	801,000	2,326,000
1969	951,000	1,195,000
1971	1,667,000	2,033,000
1972	1,930,000	1,777,000
1973	1,190,000	396,000
1974	1,195,000	1,715,000
1975	1,403,000	1,516,000
1976	1,336,000	1,768,000
1977	1,143,000	139,000

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