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Sport and Commercial Fishing:
Effects on Rehabilitation of Lake Trout
in Lake Michigan**

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THE DYNAMICS OF COMPETITION BETWEEN SPORT AND
COMMERCIAL FISHING: EFFECTS ON REHABILITATION
OF LAKE TROUT IN LAKE MICHIGAN¹

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Abstract

Hatchery-reared lake trout (Salvelinus namaycush) have been planted annually in Lake Michigan since the mid-1960's. These planted fish now support both sport and commercial fishing but have failed to reproduce successfully. One concern is that the level of fishing has increased to the point of threatening the goal of rehabilitating the stocks. We developed a mathematical simulation model to study the interactions between sport fishing, commercial fishing, and rehabilitation. The model was derived from a conventional dynamic pool model, but contains additional features which allow the analyst to simulate the planting of variable numbers of yearling fish each year, to compute the individual yields for sport and commercial fishing groups who compete simultaneously for the same stock, to apply a handling mortality factor to sublegal fish caught and released, and to compute the number of fish remaining in the stock along with their annual egg production. Our assessment focused on the effect of exploitation by one fishing group on the yield of the other group and on the effect of all fishing on the egg production of the stock. The lake trout population in the Frankfort to Good Harbor Bay area of the lake was used as a case study. The instantaneous fishing mortality for the sport fishery was 0.15 from 1972 to 1975 and 0.22 from 1976 to 1978. The commercial fishery began in 1979, and the combined fishing rate for sport and commercial fishing was 0.42 from 1979 to

1981. Mail survey estimates showed a decline in sport catch of about 50% from 1978 to 1981 while sport effort remained relatively constant. The model analysis showed that competition from the commercial fishery was the most likely reason for this decline in sport catch. If the combined fishing mortality rate remains at 0.42, egg production will decrease from a high of 45 million in 1978 to 20 million during the 1980's. Tests of different fishing regulations showed that egg production could not be substantially improved by imposing catch restrictions on one fishing group and not the other. Many of the fish protected did not survive to reproduce but were caught by the unrestricted fishing group. Joint regulations benefited egg production a great deal, but the restrictions necessary for successful rehabilitation were severe. The survival rate of lake trout in their first year of life was unknown, but simulations were conducted for selected management schemes using a reasonable range of survival rates from 0.05 to 0.005. Rehabilitation was defined for the simulations as the production of 25,000 wild fish of age 4, the approximate number now produced by stocking 100,000 yearlings. Only the complete closure of both the sport and commercial fisheries allowed rehabilitation to occur in less than 25 years for the entire range of first-year survival rates. If the first-year survival rate was as high as 0.01, rehabilitation occurred in less than 25 years when a size limit of 711 mm was imposed on both fisheries and current stocking rates

were maintained. It also occurred in less than 25 years when a 660-mm size limit was imposed on both fisheries and the stocking rates were doubled. If the first-year survival rate was 0.05, rehabilitation occurred within 5 years, even if no regulations were applied to either fishery. However, such a high survival rate is probably too optimistic.

Introduction

Native lake trout (Salvelinus namaycush) stocks became extinct in Lake Michigan by about 1956 (Wells and McLain 1973). The cause of their demise was probably the combined effects of intensive commercial fishing (Van Oosten 1949; Smith 1968) and sea lamprey (Petromyzon marinus) predation (Hile et al. 1951; Eschmeyer 1957). Since the early 1960's federal and state governments have conducted vigorous programs to control the sea lamprey and to restock lake trout. These planted lake trout exhibited good growth and survival, and a substantial sport fishery developed by the early 1970's. Commercial fishing was prohibited under regulations issued by the State of Michigan, but by 1979, a significant commercial fishery was established by various American Indian communities who fished under the rights granted them in 19th century treaties.

Competition between sport and commercial fishermen has been intense, and other problems complicate the issue further. The large stock of planted lake trout have not yet reproduced successfully. (All the planted fish bear a characteristic fin clip, so each year class can be recognized.) A few naturally produced offspring have been detected as fry, but none as adults (Wagner 1981). Also, the body tissues of the trout contain toxic substances (Merna 1979, Great Lakes Fishery Laboratory 1981). Recent laboratory experiments suggested these contaminants may be an important factor in the failure of lake trout to

reproduce successfully (Great Lakes Fishery Laboratory 1981). However, many other plausible explanations for the failure of reproduction have been advanced (Rybicki and Keller 1978, Dorr et al. 1981).

The ultimate goal of planting hatchery fish and controlling sea lamprey was to re-establish populations of lake trout with self-sustaining natural reproduction (Great Lakes Fishery Commission, policy statement adopted June 14, 1976). The work toward achieving this goal has been termed "lake trout rehabilitation." Recently, it has been suggested that the combined effects of sport and commercial fishing, along with the failure of hatchery fish to reproduce, may make this goal unattainable or even undesirable for Lake Michigan. Some work has been done to re-evaluate the practicality of the goal (Brown 1981).

The purpose of this study was to represent the population dynamics of lake trout in a computer simulation model and to use the model as an instrument for focusing on the interactions of sport fishing, commercial fishing, and rehabilitation. Hopefully, the study will serve to advance the problem of lake trout management toward a solution by providing information to enhance negotiations and decision making and by identifying avenues for future research.

Model Description

To analyze this lake trout problem, a population dynamics model was needed which gave the ability: 1) to

plant variable numbers of yearling fish and to follow each cohort thus produced throughout its lifetime; 2) to study the competition between two separate fisheries acting on the same stock; 3) to study the impact of handling mortality for fish caught and released between the size of first vulnerability of the fishing gear and the legal size of harvest; 4) to study the impact of fishing on potential egg production of the stock; and 5) to estimate how the catch and yield of each of the competing fisheries are affected by changes in fishing intensity and minimum size-limit regulations.

Our approach was to incorporate the features of interest into a standard fisheries model (Beverton and Holt 1957). In the standard yield-per-recruit model, the change in numbers in a cohort and the change in catch from the cohort with respect to age (or time) is:

$$\begin{aligned}
 (1) \quad dN/dx &= -MN, & x_r < x < x_c, \\
 (2) \quad dN/dx &= -(F + M) N, & x > x_c, \\
 (3) \quad dC/dx &= FN, & x > x_c,
 \end{aligned}$$

where: F = instantaneous fishing mortality, M = instantaneous natural mortality, N = size of cohort in numbers, C = harvest in number, x_c = age at entry into the exploited stock, and x_r = age when fish first become vulnerable to the fishing gear.

This general model was modified to incorporate the features of interest. First, we considered each cohort

separately because their initial number varied according to the number of fish planted annually. Second, we defined two separate values for F , x_r and x_c , and the catches (C) they produced. Third, we added another mortality component to account for handling or hooking mortality which occurred between ages x_r and x_c . It was defined as the instantaneous handling (or hooking) mortality rate (H). Two separate values of H were defined for each of the competing fisheries.

The revised model was defined by the following series of differential equations:

$$\begin{array}{ll}
 (4) & dN/dx = -MN, & x < x_{r,1} \\
 (5) & dN/dx = -(M + H_1) N, & x_{r,1} \leq x < x_{r,2} \\
 (6) & dN/dx = -(M + H_1 + H_2) N, & x_{r,2} \leq x < x_{c,1} \\
 (7) & dN/dx = -(M + F_1 + H_2) N, & x_{c,1} \leq x < x_{c,2} \\
 (8) & dN/dx = -(M + F_1 + F_2) N, & x_{c,2} \leq x \\
 (9) & dC_1/dx = F_1 N, & x_{c,1} \leq x \\
 (10) & dC_2/dx = F_2 N, & x_{c,2} \leq x \\
 (11) & dJ_1/dx = F_1 N, & x_{r,1} \leq x < x_{c,1} \\
 (12) & dJ_2/dx = F_2 N, & x_{r,2} \leq x < x_{c,2}
 \end{array}$$

where F_1 and F_2 were the instantaneous fishing mortality rates for two different fisheries, H_1 and H_2 were the instantaneous handling mortality rates for the two fisheries, $x_{r,1}$ and $x_{r,2}$ were the ages when fish first became vulnerable to each fishery, $x_{c,1}$ and $x_{c,2}$ were the ages at which each fishery began to harvest fish, C_1 and C_2

were the harvests in numbers for each fishery, and J_1 and J_2 were the number of fish caught and released for each fishery.

Notice the order of equations (4) through (8) assume $x_{r,1} < x_{r,2} < x_{c,1} < x_{c,2}$, but other situations such as $x_{r,1} < x_{c,1} < x_{r,2} < x_{c,2}$ are also possible with slight rearrangement of the equations. That is, one fishery may begin to harvest fish at an age which is either below the age of vulnerability for the type of gear used by the other fishery or is below the legal minimum size limit for the other fishery. However, the equations make no sense at all if $x_{c,1} < x_{r,1}$ or $x_{c,2} < x_{r,2}$, that is, fish cannot be harvested by a given fishery at ages younger than the age at which they become vulnerable to their respective fishing gears.

The solutions to the differential equations (4) through (12) were presented in Appendix A. These solutions describe the mortality of only a single cohort over its life span, but it was a simple matter to expand N from a single number to a matrix in which all the living cohorts were treated separately by age. A modern computer has no problem with such computations. However, the solutions only deal with numbers of fish and various types of mortality they sustain, and because we wanted information on yield in weight and egg production, we expanded the model further.

We used the von Bertalanffy growth curve to relate length and age of each cohort and then structured our

computer program in a manner similar to that suggested by Tyler and Gallucci (1980). Appendix B describes the method we used to compute yield. These yield computations give approximately the same results as would be obtained in a standard Beverton and Holt yield equation. We chose the Tyler and Gallucci approach because it was easily adapted to our needs in this particular problem.

We computed egg production (EGGS) for each year of simulation by the following equation:

$$(13) \text{ EGGS} = \left[(0.5) N_{i+1} \bar{W}_{i+1} \text{ FM}_i \text{ EC} \right]$$

where the 0.5 was the result of assuming equal numbers of males and females, N_{i+1} was the number of fish of age $i+1$, \bar{W}_{i+1} was the mean weight of a fish of age $i+1$, FM_i was the proportion of females mature at age i , and EC was the mean egg content per unit of female biomass. With this calculation added, our model now contained all the features of interest. A computer program was written to solve the equations.

The model requires most of the same assumptions of a typical Beverton and Holt model. Natural mortality and growth rates are constant and not affected by fishing. Mortality and growth occur continuously and simultaneously. All fish older than x_r have the same catchability. However, the assumption concerning recruitment is different. Recruitment varies with the number of yearling fish planted each year of simulation. Also, we can manipulate natural

reproduction by assigning different levels of mortality to the eggs produced by the parent stock.

There are further assumptions concerning the competition between two fisheries or gear types. Ricker (1975) defines three different types of gear competition. Our model assumes Ricker's type 1 competition. That is, the units of gear are randomly scattered over the fishery, so that all fish are exposed to capture and there is no possibility of localized depletion of the stock. Further, the units of gear do not interfere with each other in respect to the mechanics of their operation. In this situation, a unit of gear catching fish at an early age or time of year will reduce both its own catch and the catch of other gears (or competing fishermen) at an older age or later time of the year.

Simulating the History of the Fishery, 1966 to 1979

We chose the lake trout fishery in the Frankfort - Good Harbor Bay area of Lake Michigan (statistical district MM5) for a case study (Fig. 1). This area of the lake supports a significant sport fishery (Rybicki and Keller 1978) and is also part of the area ceded to Indian tribes in 19th century treaties. Indian commercial fishing was probably insignificant prior to 1979, but increased dramatically that year when the United States District Court decided Indians could fish without regulation by the State of Michigan. The study area is approximately midway between areas to the

south which are more heavily fished by sport fishermen and areas to the north which are more heavily fished by commercial fishermen.

In this section, we used the model and early data for the fishery to develop a quantitative history of the lake trout population in the study area. Our historical simulation covered the period from 1966, when yearling lake trout were first planted to re-establish the population, to 1979, when commercial fishing intensified. Thus, it described only the building of the stock and sport fishery. The impact of commercial fishing and the future of the lake trout population will be addressed later.

Parameter estimation

Data on growth, mortality, and percent females mature were either taken directly from Rybicki and Keller (1978) or from additional unpublished data available at the Charlevoix Great Lakes Station, Michigan Department of Natural Resources (Table 1).

Rybicki and Keller (1978) estimated total mortality rate (Z) of lake trout older than age 4 to be about 0.50. Assuming these fish were fully recruited, natural mortality (M) was about 0.30 and sport fishing mortality (F) was about 0.20. They estimated the natural mortality rate (M) of pre-recruits to be 0.46. Data collected more recently have given an improved estimate of natural mortality in the recruited stock of 0.36 (Ad Hoc Working Group 1979) which

indicates fishing mortality rate was actually closer to 0.15. We used these improved estimates of mortality in our simulation from 1966 to 1975, the period covered by Rybicki and Keller's data. However, we found an increase in total mortality rate ($Z = 0.58$) for the period 1975 through 1978 (Fig. 2). We assumed this was due to an increase in fishing mortality from increasing effort and/or efficiency of the sport fishery. We kept the natural mortality rate at 0.36 and increased the fishing mortality rate to 0.22 in our simulation from 1976 to 1979.

Mean lengths at age (Table 1) were computed from May and June gill net samples available at the Charlevoix Great Lakes Station. Samples covered the period 1971 to 1981, but spring samples were conducted in MM5 for only seven of those years. The approximate mean length of planted lake trout (150 mm) was assumed to represent the mean length at age 1. Mean lengths of ages 2 through 5 were excluded because of possible gear selectivity at those ages. We assumed all mean lengths were close to the mean lengths at annulus formation, because they were collected in the spring. Growth coefficients for the von Bertalanffy equation were estimated for the data using an iterative procedure (Rafail 1973). The result was $L_{\infty} = 865$ mm, $K = 0.2366$, and $x_0 = 0.1947$. Lengths predicted by the von Bertalanffy equation were converted to weights using the relationship,

$$\ln(W) = -19.179 + 3.122 (L),$$

where W is weight in kilograms and L is length in millimeters.

The percent of females mature at each age (Table 1) was taken directly from Rybicki and Keller (1978). In addition, we assumed mature females would produce 1,850 eggs per kilogram (Eschmeyer 1955).

The legal minimum size limit for lake trout was 254 mm, but according to Rybicki and Keller (1978), few fish below 580 mm were harvested by sport fishermen in northern Lake Michigan. Creel censuses conducted in 1978 and 1979 to study coho salmon (Patriarche 1980) confirmed their assertion (Fig. 3). About 27% of this catch was taken in April and May, 48% in June, 15% in July, 7% in August, and 3% in September to December. Unfortunately, only about 6% of the data were taken directly from statistical district MM5, and the rest were heavily weighted towards the southern waters of the lake (about 75% from districts MM7 to MM8). Nonetheless, we assumed this data gave a fair representation of the length-frequency of the catch in MM5.

It appears that lake trout recruited into the fishery gradually, over about a 460-mm to 610-mm length range, although this is difficult to determine with certainty because we do not know the length frequency of the population. Fish over 610 mm in length made up 70% of the catch and were probably represented in numbers that closely related to their abundance in the population. Our model does not allow gradual recruitment over a range of sizes,

but it uses knife-edged recruitment at a specified age. It seemed unlikely that including the details of gradual recruitment in the model would affect the results very much. Thus, we used the weighted mean length for fish in the 460-mm to 610-mm length range as the effective minimum size limit for sport fishery. The result was an age of entry (x_c) of 4.3 years at a length of 540 mm. Ad Hoc Working Group (1979) used a similar age of entry in their calculations.

We assumed the number of lake trout caught and released by sport fishermen was small enough to be considered negligible. Therefore, the age of first vulnerability (x_r) was set at 4.3 (540 mm), the same as the age of entry into the exploited stock (x_c), and the instantaneous hooking mortality rate was set to zero.

Finally, for the historical simulation, we assumed natural reproduction was unsuccessful, that is, none of the eggs produced by the adult stock survived to age 1. The simulated population was maintained by stocking yearlings each spring (Table 2).

Results

Results of simulating the lake trout population from 1966 to 1979 showed a period of rapid increase in catch and yield for the sport fishery from 1969 to 1972, a period of relatively constant catch and yield from 1972 to 1975, a substantial increase in catch and yield in 1976, and a

period of relatively constant catch and yield from 1976 to 1978 (Fig. 4). The trend in catch was fairly close to the trend shown by Michigan's annual mail survey of sport catch. However, as Rybicki and Keller (1978) showed, the estimated catch from the mail survey was about ten times too high in MM5. The major difference between the trend produced from the model and the trend produced from the mail survey was in the year 1976. The model showed a sharp increase in catch in 1976, whereas the mail survey showed the increase in catch occurred in 1977. This difference was probably the result of assuming a constant fishing mortality rate ($F = 0.15$) in the model from 1969 to 1975, and then assuming the rate increased to $F = 0.22$ in 1976 and remained constant thereafter. The latter fishing mortality rate was actually a 3-year average for 1976 through 1978, and it could easily be higher than the actual rate for 1976. In contrast, the mail survey estimates of catch reflected annual fluctuations in fishing effort.

A relatively small number of eggs should have been produced as early as the fall of 1969 (Table 3). The actual existence and eventual fate of these eggs has been the focus of many research projects in recent years (Rybicki and Keller 1978, Brown et al. 1981, Dorr et al. 1981, Great Lakes Fishery Laboratory 1981, Wagner 1981).

Peck (1980) estimated the average survival of lake trout eggs from deposition to the button-up fry stage was 12% on a Lake Superior reef. If we assume the eggs produced

by this Lake Michigan stock were deposited and had a similar survival rate to the fry stage, we can estimate the number of fry that should have been produced each year (Table 3). Furthermore, we can speculate as to the time these wild fish could have been detected by standard monitoring methods.

With stocking rates averaging about 100,000 yearlings per year, 10,000 wild yearlings would represent 9% of any given year class. Considering the precision of our sampling and fin clipping techniques (Rybicki and Keller 1978), it seems fair to assume that this proportion of wild fish in a year class would be near the minimum level we could detect. Fry production under the given assumptions would not have been significant until at least 1972 (Table 3). Then, an annual survival rate of 0.004 would have produced 10,000 wild yearlings in 1973. If they actually existed, these wild fish might have been detected in trawl samples that year, but would not have appeared in gill net samples until at least 1974 at age 2. They may not have appeared with a statistically valid sample size until 1976 at age 4. Thus, even under favorable biological and environmental conditions, it seems unlikely that natural reproduction of lake trout could have been detected before 1975 or 1976, and any problem causing poor conditions for reproduction could have easily delayed the date of detection into the 1980's. In fact, our analysis suggests that poor conditions must have existed. The adult stock appeared large enough to

reproduce a detectable number of progeny, and yet none were detected.

Future of Fishery without Regulation

In the previous section, we showed the development of the sport fishery over time (Fig. 4). Now we will show how competition from the commercial fishery is likely to affect the situation. In order to do this, we made several assumptions. First, stocking of lake trout was maintained at about 100,000 yearlings per year. Second, lamprey control efforts were maintained at current levels. Third, the parameters for the sport fishery ($x_{r,1} = 540$ mm, $x_{c,1} = 540$ mm, $F_1 = 0.22$) were held in constant throughout the period. And finally, the parameters for the commercial fishery for x_r and x_c were the same as those for the sport fishery during the period (that is, $x_{r,2} = 540$ mm, $x_{c,2} = 540$ mm). The fishing mortality rate for the commercial fishery was varied.

Results of simulation showed that the commercial fishery had a substantial impact on the sport fishing catch, even at relatively low rates of fishing (Fig. 5). With no commercial fishing at all ($F_2 = 0.0$), the sport catch stabilized at 7,800 fish per year. With a commercial fishery operating at a fishing rate of only 0.1, the sport catch declined 15% to 6,600 fish. Sport catch declined 41% to 4,600 fish for a moderate commercial fishery operating at

$F_2 = 0.4$, and for a relatively intense commercial fishery of $F_2 = 0.8$, it declined 58% to 3,300 fish.

The annual yield in weight for the commercial fishery increased as the commercial fishing rate increased (Fig. 6). The commercial yield was at a maximum in 1979 and declined until about 1985 in all simulations. After 1985 the commercial yield stabilized at different levels, depending on the fishing rate. In reality, the fishing rate for the commercial fishery was probably lower in 1979 than in 1980 and 1981, because the fishery was just beginning to intensify. Thus, the actual trend in yield did not show a sharp peak in 1979, but peaked in 1980 and is currently on the decline.

The level at which the commercial fishery finally stabilized in the simulations can be considered the equilibrium yield for the given fishing rate (Fig. 6). This increased asymptotically to 32,000 kilograms as fishing rate increased. This asymptote represents the maximum sustained yield for the commercial fishery under the assumed rates of mortality, growth, and stocking, but it could only be approached by instantaneous fishing rates greater than 1.5.

Increasing the exploitation had a dramatic effect on the number of eggs produced (Fig. 7). Production stabilized at 40.6 million eggs when no commercial fishery was operating, declined 31% to 27.9 million eggs when the commercial fishery was operating at a rate of only 0.1, and declined by 90% to 9 million eggs when the commercial

fishery was operating at 0.8. Clearly, egg production in lake trout population is very sensitive to exploitation.

It is impossible to determine the accuracy of these predictions. For one thing, it seems unlikely that the sport fishery would continue at the same level ($F_1 = 0.22$) if the commercial fishery intensified to 0.80 and higher. Furthermore, we cannot predict the actual level of sport or commercial fishing into the future. The best we can do is compare data available from 1979 through 1981 with model predictions.

The actual sport fishing effort, as measured by the mail survey, has remained relatively constant in the study area for the period from 1976 through 1981, but a reduction in the daily possession limit from 5 to 3 fish was put into effect in 1979. The estimated sport catch from the mail survey (divided by 10) was 8,600 fish in 1979, 3,000 fish in 1980, and 4,400 fish in 1981. The relatively high catch in 1979 is puzzling. Both the reduction in the possession limit and the build-up of the commercial fishery (Fig. 5) occurred in 1979, and this should have caused a reduction in sport catch that year. The decrease in catch of about 50% in 1980 and 1981 agreed more closely with our expectations, but it cannot be determined with certainty whether this reduction in catch was due to the possession limit, the commercial fishery, or both. However, closely monitored experiments in trout stream fisheries have been consistent in finding that possession limits have no effect on the

total annual catch (Hunt 1970, Latta 1973). Thus, the commercial fishery is the most likely reason for the decline in sport catch.

Catch records furnished by Indian fishermen indicated they harvested 15,800 kilograms in 1979, 25,600 kilograms in 1980, and 22,700 kilograms in 1981 (Richard Hatch, U.S.F.W.S., personal communication). According to the model prediction, it would be necessary for the commercial fishery to be operating with an instantaneous fishing rate of about 0.30 or 0.40 for them to obtain annual yield of this size (Fig. 6). However, the simulations did not consider the possibility that the possession limit on the sport fishery might have reduced the fishing mortality rate of that fishery. If it had done so, the commercial fishery could have harvested the quantities of fish they reported with a lower fishing rate, perhaps as low as 0.20.

Data from fall gill-net samples collected by the Charlevoix Great Lakes Station showed total instantaneous mortality (Z) increased to 0.78 for the 1979 through 1981 period (Fig. 8). Assuming the natural mortality rate remained constant at 0.36, this leaves a total fishing mortality rate of 0.42 to be divided between the sport and commercial fisheries. If one assumes the sport fishing mortality decreased somewhat because of the possession limit, then the commercial fishing rate was somewhat higher than 0.20. However, almost any reasonable assessment would

conclude that both fisheries were operating at rates of roughly the same magnitude, about 0.20 for each.

Management Alternatives

The outcomes of different management alternatives will be defined in terms of the change in yield experienced by both fisheries and the effect on lake trout egg production. Management alternatives may be fairly numerous, but not all are practical. We will examine a series of alternatives based on different combinations of minimum size limits and annual catch quotas.

Minimum size limits on the sport fishery and annual catch quotas on the commercial fishery are probably the most practical management alternatives at the present time, considering the current fishing methods. Controlling fishing effort of the sport fishery to meet annual catch quotas does not seem practical. Many individual fishermen participate in the fishery, and it would be difficult and expensive to monitor the fishery on a day-to-day basis. Controlling the age of entry of the commercial fishery does not seem practical either, at least not as long as the Indians are using gill nets as their primary gear. Even when the mesh size of a gill net is increased, many small lake trout are caught by their teeth (Haas 1978).

A size limit on the sport fishery and a catch quota on the commercial fishery may be the most practical alternatives, but they are not without problems. Perhaps

the most serious of these problems for the sport fishery is the lack of information on the survival of lake trout after hook and release; and for the commercial fishery, the interaction of lake trout quotas with those of whitefish. Lake trout and whitefish are often caught in the same gill net, so if the quota for one of the species is reached, it is not possible to continue fishing for the second species without exceeding the quota of the first.

Rybicki and Keller (1978) were of the opinion that hooking mortality would not be a major problem in the sport fishery. They suggested raising the size limit on lake trout to 610 mm. Wydoski (1980) reported an average mortality of 6%, with a range of 2 to 43% for fish hooked on artificial lures (the way most lake trout are caught). These figures included all the values he could find in the scientific literature and included a wide variety of species and conditions. The one experiment on lake trout (Falk et al. 1974) showed that 7% of the fish died from hooking. However, the actual hooking mortality in the Lake Michigan sport fishery could easily be much higher than this. During the summer, lake trout are usually hooked at great depths, where water temperatures are cold and pressure is high; then, they are brought rather quickly to the warmer surface waters where pressure is low. These temperature and pressure changes may reduce their ability to survive the handling stress involved with capture.

It is possible to use the simulator to gain insight into the impact of hooking mortality on the effectiveness of minimum size limits. For the sake of illustration, we assumed the fishing mortality rates for each fishery would increase to 0.30 and remain constant into the future. The ages of first vulnerability ($x_{r,1}$ and $x_{r,2}$, where hooking mortality begins, were both held constant at 4.3 (540 mm), and only the hooking mortality rate for the sport fishery was varied. The commercial fishery began harvesting at age 4.3 (540 mm) in all simulations. Hooking mortality was examined at three size limits for the sport fishery, 540 mm (age 4.3), 635 mm (age 5.8), and 760 mm (age 9.1). These size limits span the practical range of application for such a regulation.

Increasing hooking mortality in the sport fishery reduced the yields of both the sport and commercial fisheries by about the same relative amount, but as might be expected, the impact was less significant for lower size limits (Fig. 9). In this comparison, hooking mortality was only responsible for differences in the slopes of the lines. The minimum size limits were responsible for differences in the elevation of the lines. The instantaneous hooking mortality rate used in the model was the product of the proportion dying after catch and release and the instantaneous fishing mortality rate (Clark 1983).

No reduction in yield occurred at the 540-mm size limit (Fig. 9), because it was assumed that this was the minimum

size of vulnerability to the fishing gear. A 28% reduction in yield was observed at a 635-mm size limit, when the percent of fish dying after catch and release was increased from 0 to 100. A 39% reduction in yield was observed over the same range in hooking mortality for a 760-mm size limit. Thus, hooking mortality may affect management schemes which seek to allocate the total yield through size limit regulations.

Increasing hooking mortality in the sport fishery also reduced the effectiveness of minimum size limits in benefiting egg production (Fig. 10). Once again, the impact was greater with higher size limits. It should be noted, however, that substantial gains in egg production were achieved by increasing the size limit, even when hooking mortality was fairly high. For example, even when the hooking death rate was as high as 50%, egg production increased by 23% when the size limit was increased from 540 mm to 635 mm, and it increased by 54% when the size limit was increased to 760 mm.

Keeping in mind the fact that hooking mortality and interactions with the whitefish fishery may have a significant impact on the results, we simulated the application of four different management alternatives: (1) imposing a size limit on the sport fishery without regulating the commercial fishery; (2) imposing a quota on the commercial fishery without regulating the sport fishery; (3) maintaining equal yields for both fisheries via

a size limit on the sport fishery and a quota on the commercial fishery; and (4) maintaining equal yields for both fisheries via a size limit on both fisheries. The first three alternatives could be applied to the real-world fishery immediately, but the fourth alternative could be applied only if the commercial fishery converts from gill nets to impoundment gear.

The results were again presented in terms of the impact on the yields for each fishery and on the egg producing potential of the lake trout population. In these simulations, we assumed the death rate for fish caught and released was 30% in the sport fishery. Also, we continued to assume the fishing rates for both fisheries would be 0.30 unless the management scheme required a reduction, as it did when a quota was imposed. The ages of vulnerability ($x_r = 4.3$) and entry ($x_c = 4.3$) remained the same as for previous simulations unless the management scheme required an increase in the age of entry, as it did when a minimum size limit was imposed.

Size limit on sport fishery

Under the assumption of constant fishing rates for both fisheries ($F_1 = F_2 = 0.30$), the yield for the sport fishery decreased as the minimum size limit increased (Table 4). The commercial fishery benefited from the restrictions on the sport fishery. Commercial yield increased as the minimum size limit on the sport fishery increased.

Presumably, they caught some of the fish, sublegal to the sport fishery, that survived catch and release.

Egg production increased as the minimum size limit increased and more of the parent stock was protected (Table 4), but the gains in egg production were relatively modest. For example, it would be necessary to increase the size limit from the present 540 mm to 660 mm to realize a 46% gain in egg production. At the same time, a 65% reduction in the yield to the sport fishery would occur.

Quota on commercial fishery

As the fishing rate and associated quota on the commercial fishery were reduced, the yield for the sport fishery increased, even though a constant sport fishing rate ($F_1 = 0.30$) was maintained (Table 5). The sport fishery benefited from the restrictions on the commercial fishery.

Once again, restrictions on one fishery and not the other allowed only moderate gains in egg production (Table 5). It was necessary to reduce the commercial yield by 38%, from 15,100 to 9,400 kilograms, to achieve a 58% increase in egg production, from 11.4 to 18.0 million.

Equal yields -- size limit on sport fishery, quota on commercial fishery

It was not a simple matter to estimate the fishing mortality rate for the commercial fishery which would give a yield equal to the yield of the sport fishery when the two

fisheries have different size limits. The most practical way to solve this problem was by iterative procedures. One could use trial-and-error iteration, but we used a procedure known as the Newton-Raphson method (Carnahan et al. 1969). The computer model was incorporated into a programming loop in which the fishing rate on the commercial fishery was adjusted repeatedly until the yields for both fisheries were equal. The Newton-Raphson method usually solved the problem in less than five program iterations.

Yield (or quota) for both the sport and commercial fishermen decreased as the minimum size limit on the sport fishery increased (Table 6), but it decreased less for both groups when they were managed jointly than when they were managed separately (Tables 4, 5, and 6). Managing both fisheries at the same time prevented one group from benefiting from restrictions placed on the other. For example, the sport yield for a 635-mm size limit was only 7,100 kilograms when no corresponding regulation was imposed on the commercial fishery (Table 4), but was 11,000 kilograms for the joint management scheme (Table 6).

As might be expected, regulating both fisheries at the same time benefited egg production much more than if only one of the fisheries was regulated (Table 6). Egg production increased 118% when the size limit on the sport fishery was increased from 540 mm to 635 mm and corresponding quota was placed on the commercial fishery.

Egg production was increased only 33% for a similar quota applied only to the commercial fishery (Table 5).

Equal yields -- size limits on both fisheries

Imposing equal minimum size limits on both fishing groups provided equal yields in our example, because we assumed both groups had equal fishing rates. If the fishing rates were different, it would have been necessary to impose a different size limit on each fishery to achieve equal yields.

This type of joint regulation gave essentially the same results as maintaining equal yields via a size limit on one fishing group and a quota on the other (Tables 6 and 7). The main difference between the two types of joint regulation lies in the type of fishing gear used by the commercial fishermen. As mentioned earlier, a minimum size limit would not be an effective way to manage a commercial gill-net fishery.

The Outlook for Rehabilitation

We showed that the level of fishing has a very significant impact on lake trout egg production. But the reproductive dynamics of the real population are much more complicated than was represented in the model. It is not known if enough hatchery fish are depositing their eggs on suitable spawning grounds. It is not known if the value in

terms of survival of an egg from a 4-year-old fish is comparable to that of an older fish. These and many more questions must be answered before a definitive assessment can be made. Nonetheless, management decisions concerning this valuable resource must be made immediately if past investments are to be protected.

We used the simulator to estimate the time it would take to achieve rehabilitation under selected management schemes. We assumed the survival of eggs to hatching was 12% (Peck 1981) and used levels of survival for fry-to-yearling stage of 0.05, 0.01, and 0.005. Real-world estimates of fry-to-yearling survival are not available, but we think these figures represent some reasonable possibilities. We defined the condition for rehabilitation to be the production of 25,000 wild fish of age 4, because this is approximately the number of age-4 fish currently produced by stocking 100,000 yearlings per year. We started the simulation in 1979, using the estimated number and age structure of fish for that year as the initial population.

Five management schemes were simulated with the fishing rate for each group held at 0.20: (1) continuation of current fishing regulation; (2) joint imposition of a 660-mm size limit for each fishery; (3) joint imposition of a 711-mm size limit for each fishery; (4) a doubling of the annual stocking rate combined with a jointly imposed size limit of 660 mm; (5) a doubling of the annual stocking rate combined with a jointly imposed size limit of 711 mm. A sixth scheme

was also considered--the complete closure of both the sport and commercial fisheries.

No new regulations would be needed if the survival rate in the first year was 0.05 (Table 8). The initial 1979 population would have produced enough young to achieve rehabilitation within 5 years. Clearly, the 0.05 survival rate, combined with our assumptions about reproduction, was overly optimistic, otherwise rehabilitation would have occurred by the mid-1970's.

When the first-year survival rate was 0.01, rehabilitation did not occur within 25 years unless the size limits were raised to 711 mm for current stocking rates (Table 8). However, the rate of increase in the numbers of wild fish in the population was relatively slow for this management scheme when compared to doubling the stocking rate or closing the fisheries (Fig. 11). When the survival rate was 0.005, the complete closure of both fisheries was the only management scheme to achieve rehabilitation within 25 years.

Based on these simulations, the outlook for rehabilitation is not good. The only management scheme achieving rehabilitation for all levels of juvenile survival tested was the complete closure of both the sport and commercial fisheries.

All modeling analyses suffer to some extent from deficiencies in the data and the model in reflecting the behavior of the real world. The results should be

interpreted with these deficiencies in proper perspective. Our modeling assumptions were described earlier. Most of them were probably violated to some degree, but we do not think these violations would significantly alter the results. As far as the data were concerned, growth and total mortality estimates were probably fairly good, although the use of catch curves (Figs. 2 and 8), during a period when fishing effort and mortality were expanding, violated the assumptions of that method (Ricker 1975). Dividing the data into small time periods (1975 to 1978 and 1979 to 1981) adjusted for this problem to some degree. The problem of separating total mortality into natural and fishing components was much more difficult. We relied on estimates of F and M made by other investigators. The fecundity data we used dated back to the pre-lamprey era and were from Lake Superior rather than Lake Michigan stocks (Eschmeyer 1955). Considering the changes that have occurred in the fish stock and its environment in recent years, fecundity in the current population is almost certainly somewhat different.

Better information is needed on the nature of both the sport and commercial fisheries. The death rate of fish caught and released by sport fishermen must be estimated before a definitive analysis of minimum size limits can be made. Almost no information is available about the commercial catch. The size and age structure should be

examined, and the age at first capture should be defined. Better information on the sport catch is also needed.

The survival rates we used for the egg and fry stages were probably the least reliable of all the data. Unfortunately, the practical difficulties in estimating these rates may prevent much improvement in their reliability. The survival rate from egg to age 1 will remain unknown in Lake Michigan, at least until successful reproduction has occurred for several years. In the meantime, it may be possible to estimate egg-to-age 1 survival in naturally reproducing Lake Superior stocks in the same manner as was done by Walters et al. (1980). Applying the Lake Superior rate to Lake Michigan stocks in an analysis such as this may provide further insight into the question of whether the reproductive problem lies in the environment of Lake Michigan or in a deficiency in egg production.

Our assessment of the lake trout problem focused on the competition between two fisheries acting on the same stock and the effect of their exploitation on each other and on the egg production of the population. The model we developed was useful in analyzing the problem and probably reflected the nature of the competition fairly well. This type of model may be useful in assessing other fisheries in which a single stock is shared by one or more groups. The computer program may be obtained from the senior author.

Acknowledgements

Many fishery workers employed by the State of Michigan, the United States government, and various universities have studied and debated this lake trout problem for many years. Many of our ideas were taken from their reports and publications. Most useful were the works of Rybicki and Keller (1978), who summarized most of the data available on lake trout prior to 1975, and Ad Hoc Working Group (1979), who were the first to attempt to set quotas for lake trout using a dynamic pool model. Some of our ideas came from interaction with other biologists in committee meetings sponsored by the Great Lakes Fishery Commission. Of course, we still accept the final responsibility for this report. We are grateful to many people employed by Michigan Department of Natural Resources for their assistance in the production of the report. Personnel of the Charlevoix Great Lakes Station collected most of the data on the lake trout fishery. W. Carl Latta, Myrl Keller, Ronald W. Rybicki, and James C. Schneider reviewed the manuscript and provided helpful suggestions for its improvement. Barbara A. Gould, Barbara A. Lowell, and Grace M. Zurek typed several drafts of the manuscript until the final version evolved. We are also grateful for reviews and suggestions given by Richard W. Hatch and Gary W. Eck of the United States Fish and Wildlife Service. The study was funded through Dingell-Johnson Project F-35-R, Michigan.

Table 1. Estimated natural mortality rates (M), mean lengths, and percent females mature by age for lake trout in statistical district MM5 of Lake Michigan.

Age	Natural mortality rate (M)	Mean length (mm)	Percent females mature
1	0.46	150	0
2	0.46	---	0
3	0.46	---	0
4	0.46	---	6
5	0.36	---	17
6	0.36	674	92
7	0.36	709	97
8	0.36	741	100
9	0.36	755	100
10	0.36	767	100
11	0.36	778	100
12	0.36	785	100
13	0.36	813	100
14	0.36	848	100

Table 2. Number of yearling lake trout planted each spring
in statistical district MM5 of Lake Michigan.

Year	Thousands of fish planted
1966	100
1967	102
1968	117
1969	100
1970	50
1971	70
1972	125
1973	126
1974	107
1975	85
1976	111
1977	91
1978	104
1979	101
1980	117

Table 3. Estimated egg and fry production of lake trout by year in district MM5 of Lake Michigan. The survival rate of the fry needed to produce 10,000 yearlings is listed in the column labeled S.

Year	Millions of eggs	Millions of fry	S
1969	1.6	0.0	---
1970	5.5	0.2	0.050
1971	21.0	0.7	0.014
1972	32.9	2.5	0.004
1973	41.8	3.9	0.003
1974	44.7	5.0	0.002
1975	41.5	5.4	0.002
1976	39.7	5.0	0.002
1977	43.7	4.8	0.002
1978	45.4	5.2	0.002

Table 4. Estimated sport yield, commercial yield, and egg production at equilibrium for minimum size limits applied only to the sport fishery.

Sport size limit		Sport yield (kgs)	Commercial yield (kgs)	Egg production (millions)
Length (mm)	Age			
540	4.3	15,100	15,100	11.4
559	4.6	13,300	15,800	12.0
584	4.9	11,100	16,700	13.0
610	5.4	8,900	17,500	14.0
635	5.8	7,100	18,300	15.2
660	6.3	5,300	18,900	16.6
686	6.9	3,800	19,500	18.1
711	7.5	2,600	19,900	19.4
737	8.3	1,500	20,200	20.4
760	9.1	900	20,400	21.1

Table 5. Estimated sport yield, commercial yield (quota), and egg production at equilibrium for different rates of fishing by commercial fishermen.

Commercial fishing rate (F_2)	Commercial quota (kgs)	Sport yield (kgs)	Egg production (millions)
0.30	15,100	15,100	11.4
0.25	13,500	16,100	13.2
0.20	11,600	17,300	15.4
0.15	9,400	18,700	18.0
0.10	6,800	20,400	21.2
0.05	3,700	22,200	25.1

Table 6. Equilibrium yield in weight for each fishery and lake trout egg production for the joint management of the sport and commercial fisheries. Sport fishery managed by a size limit and the commercial fishery by a quota.

Sport size limit		Commercial fishing rate (F_2)	Yield for each fishery (kgs)	Egg production (millions)
Length (mm)	Age			
540	4.3	0.300	15,100	11.4
559	4.6	0.255	14,300	13.7
584	4.9	0.210	13,300	16.9
610	5.4	0.171	12,100	20.7
635	5.8	0.141	11,000	24.9
660	6.3	0.115	9,800	29.6
686	6.9	0.091	8,500	35.6
711	7.5	0.071	7,200	41.2
737	8.3	0.052	5,700	47.6
760	9.1	0.038	4,400	53.1

Table 7. Equilibrium yield in weight for each fishery and lake trout egg production for the joint management of the sport and commercial fisheries. Each group received an equal yield and each was managed by a minimum size limit.

Size limit		Yield for each fishery (kgs)	Egg production (millions)
Length (mm)	Age		
540	4.3	15,100	11.4
559	4.6	14,300	13.0
584	4.9	13,400	15.6
610	5.4	12,200	18.9
635	5.8	10,900	23.2
660	6.3	9,600	28.6
686	6.9	8,100	36.3
711	7.5	6,600	42.8
737	8.3	5,000	50.1
760	9.1	3,700	56.1

Table 8. Estimated number of years to rehabilitation for various management schemes and first-year survival rates. Rehabilitation was defined as the production of 25,000 wild fish of age 4.

Management scheme	First-year survival rates:		
	0.05	0.01	0.005
No change	5	>25	>25
Current stocking rate and:			
660-mm size limits	5	>25	>25
711-mm size limits	5	14	>25
Double stocking rate and:			
660-mm size limits	5	11	>25
711-mm size limits	5	10	>25
Close both fisheries	5	8	17

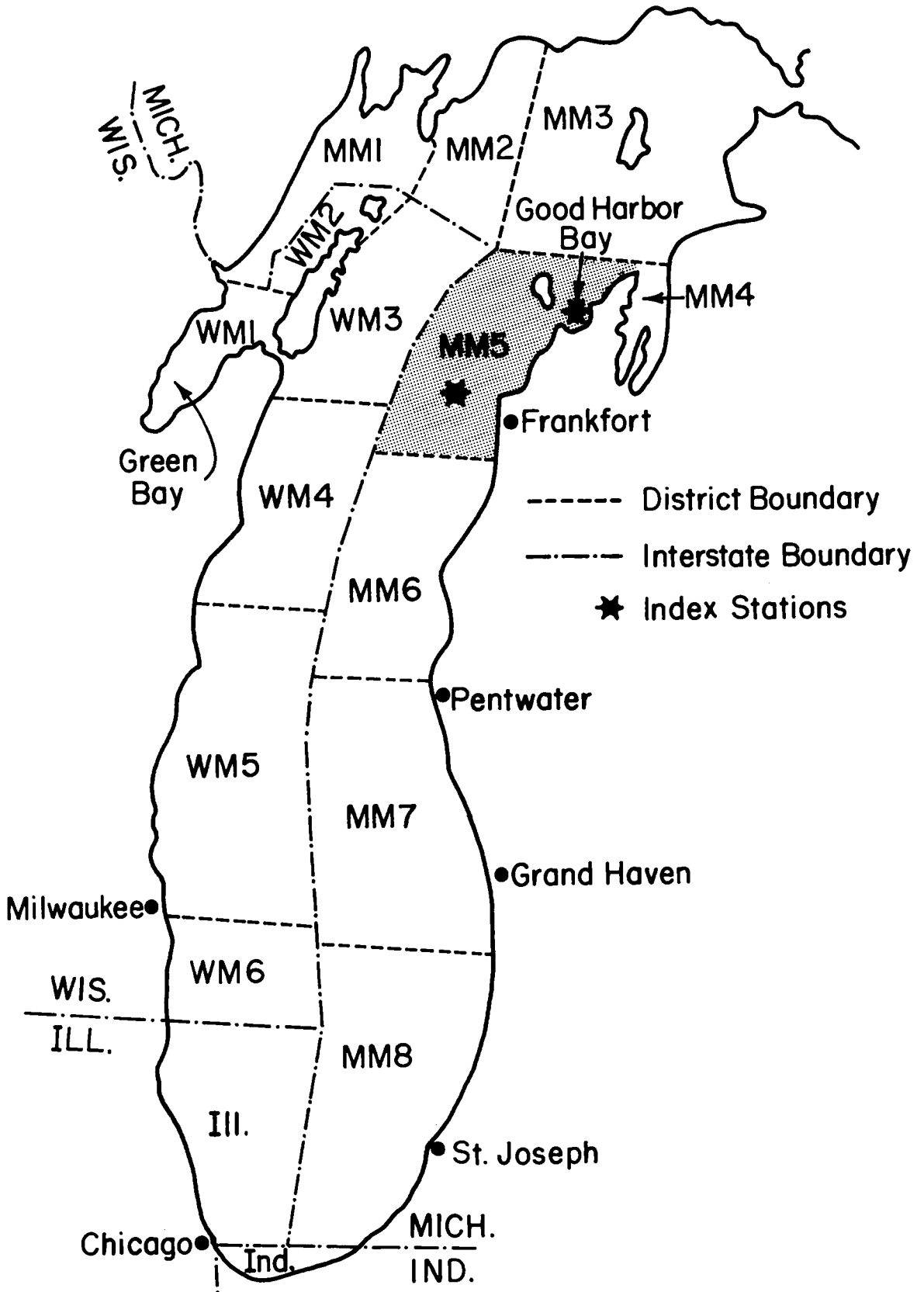


Figure 1.--Fisheries statistical districts in Lake Michigan with study area shaded. Population data were collected each year from locations shown as index stations.

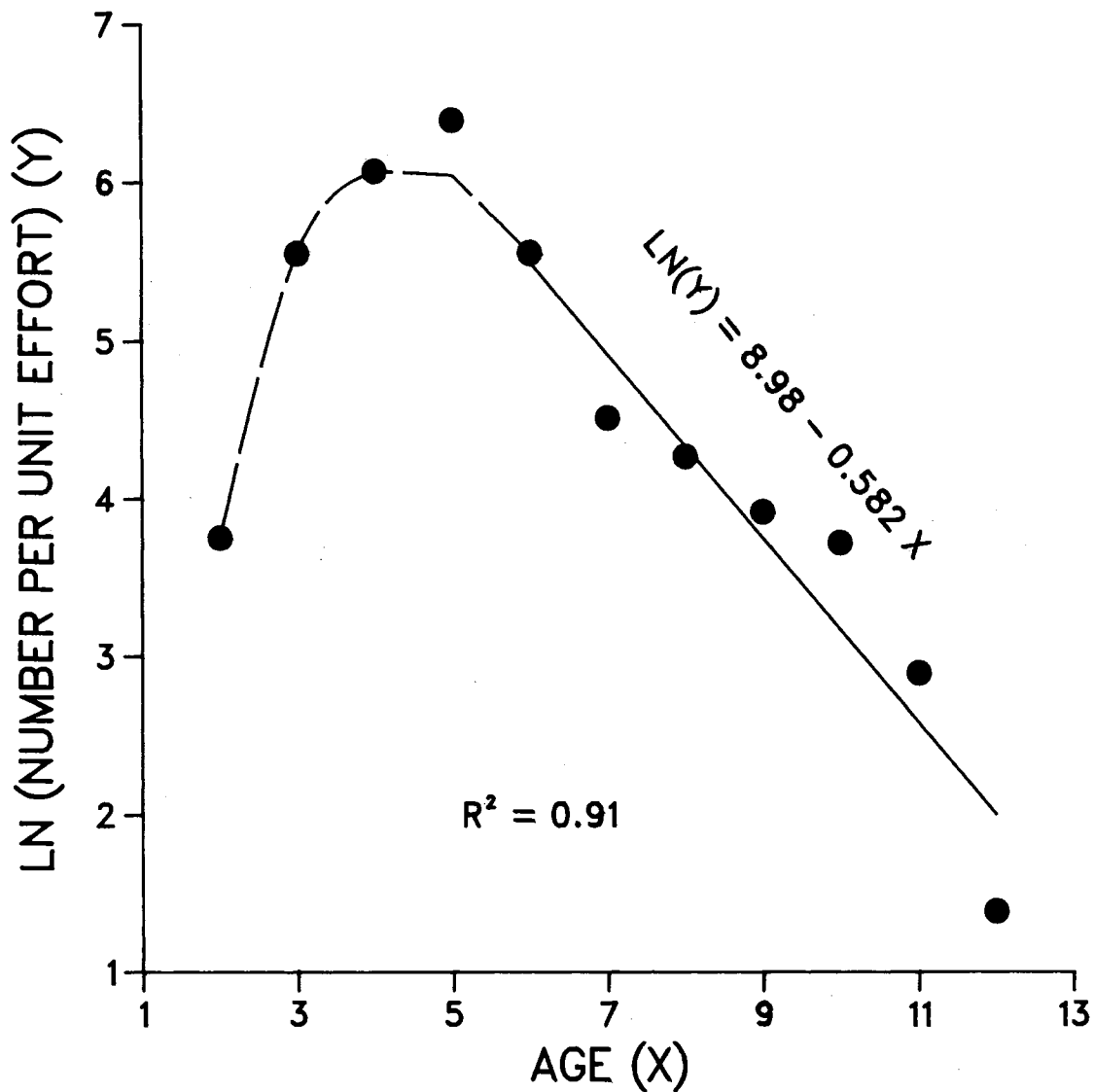


Figure 2.--Catch curve for lake trout collected during fall gill net sampling, 1975 through 1978. Cumulative effort was 33,650 meters of graded, experimental gill net fished for 24 hours. Regression was computed for fish from ages 6 to 12. The slope, 0.582, is an estimate of total instantaneous mortality rate (Z).

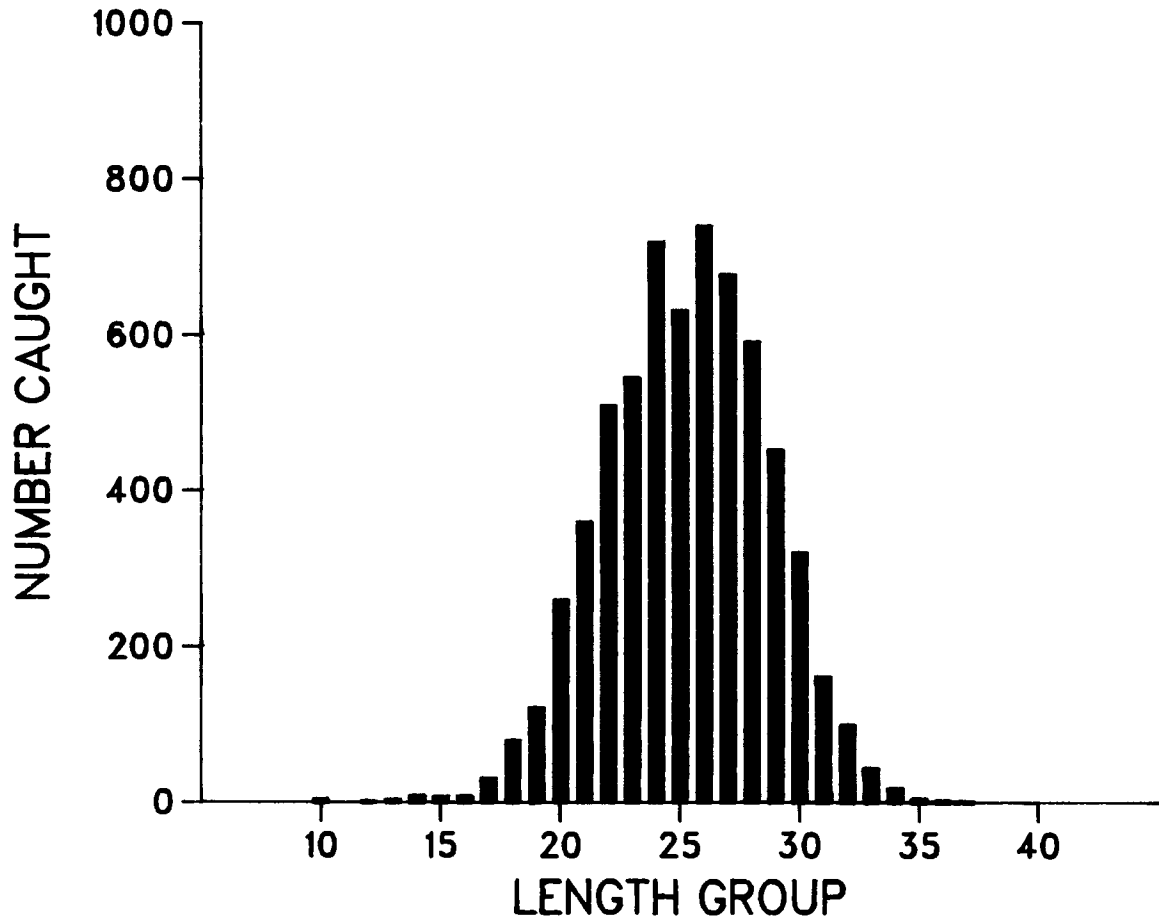


Figure 3.--Length frequency of lake trout in 1978 and 1979 sport catch from Michigan waters of Lake Michigan. Length groups correspond to inch groups where group 10 includes fish from 254 mm to 278 mm, group 11 includes fish from 279 mm to 304 mm, etc.

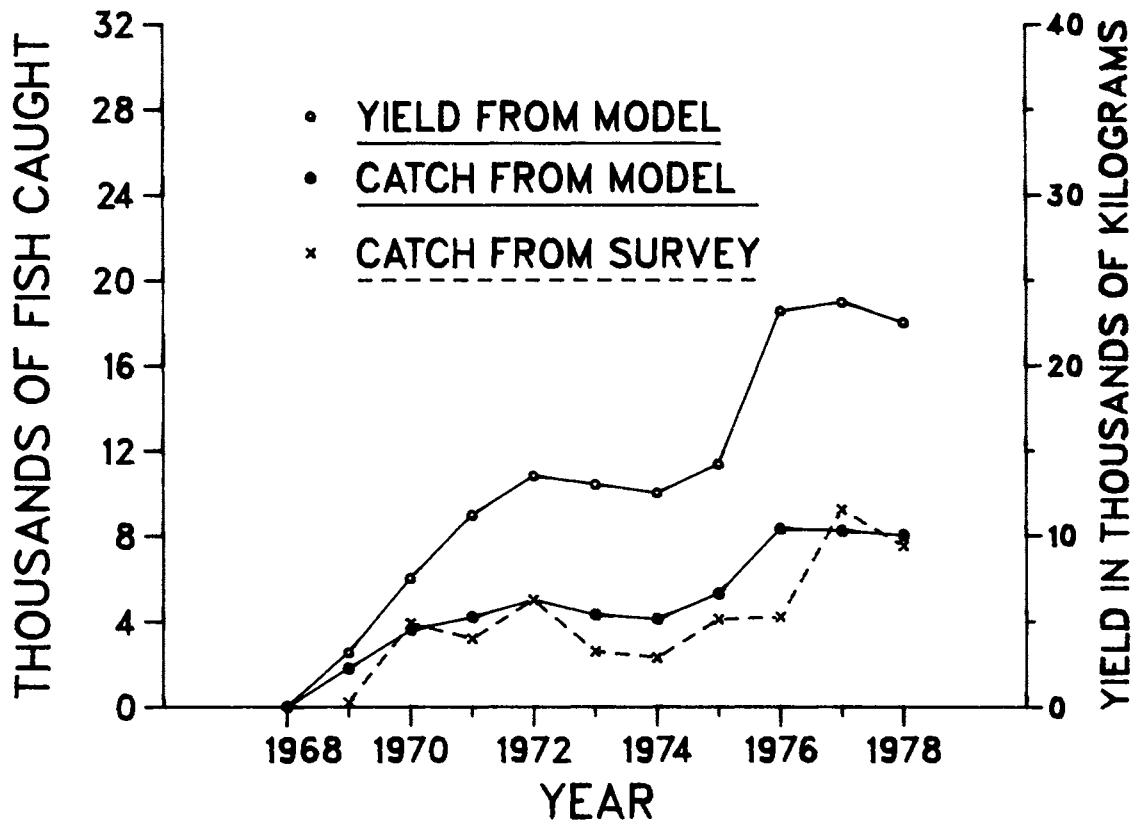


Figure 4.--Simulated yield in weight and catch in numbers for the sport fishery in district MM5 of Lake Michigan. Catch estimated from mail survey (divided by 10) is shown for comparison.

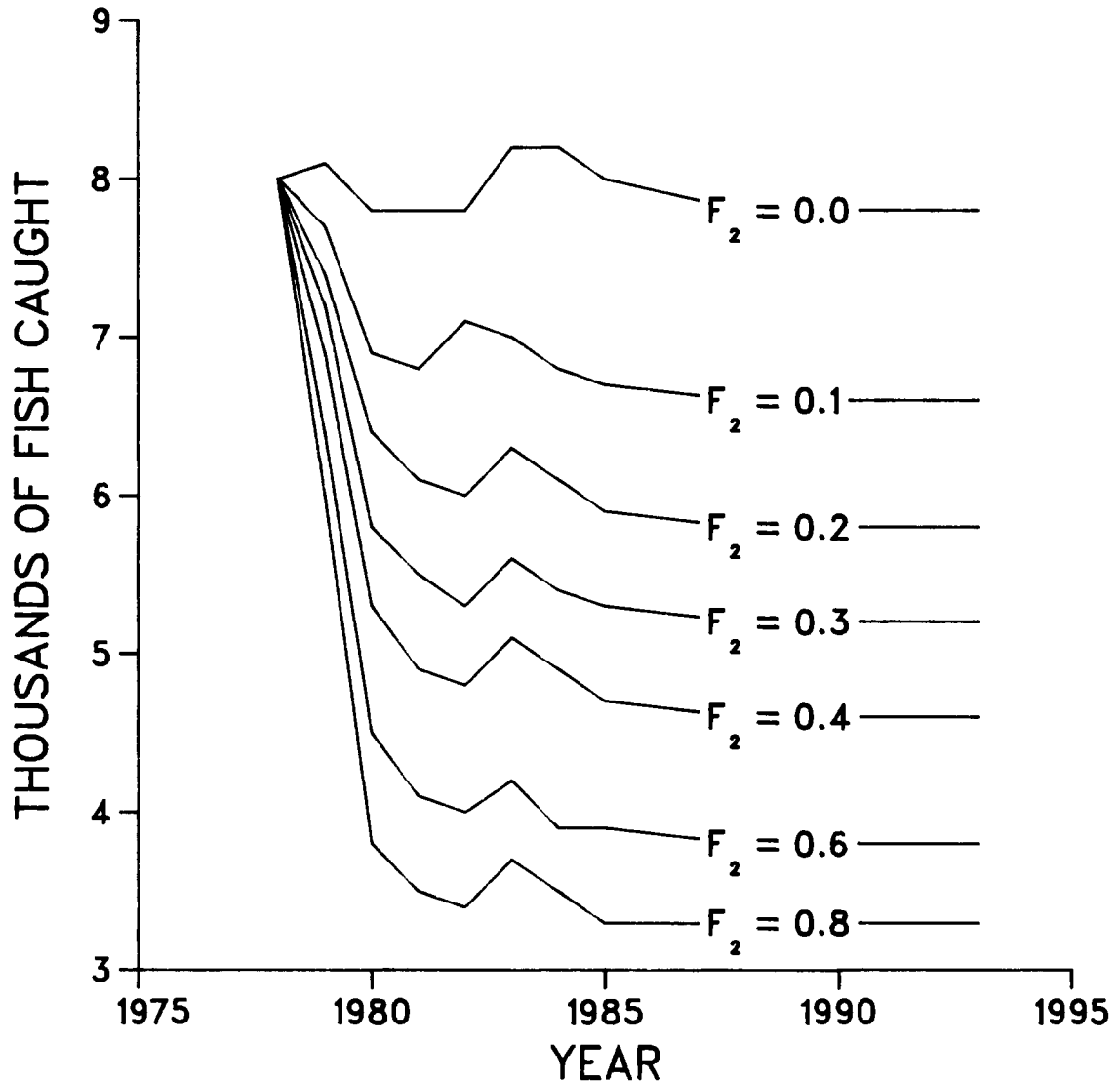


Figure 5.--Annual sport catch of lake trout predicted for various levels of competition with the commercial fishery. Fishing mortality rate for the sport fishery (F_1) was maintained at 0.22 for all simulations, while fishing mortality rate for the commercial fishery (F_2) was varied as indicated.

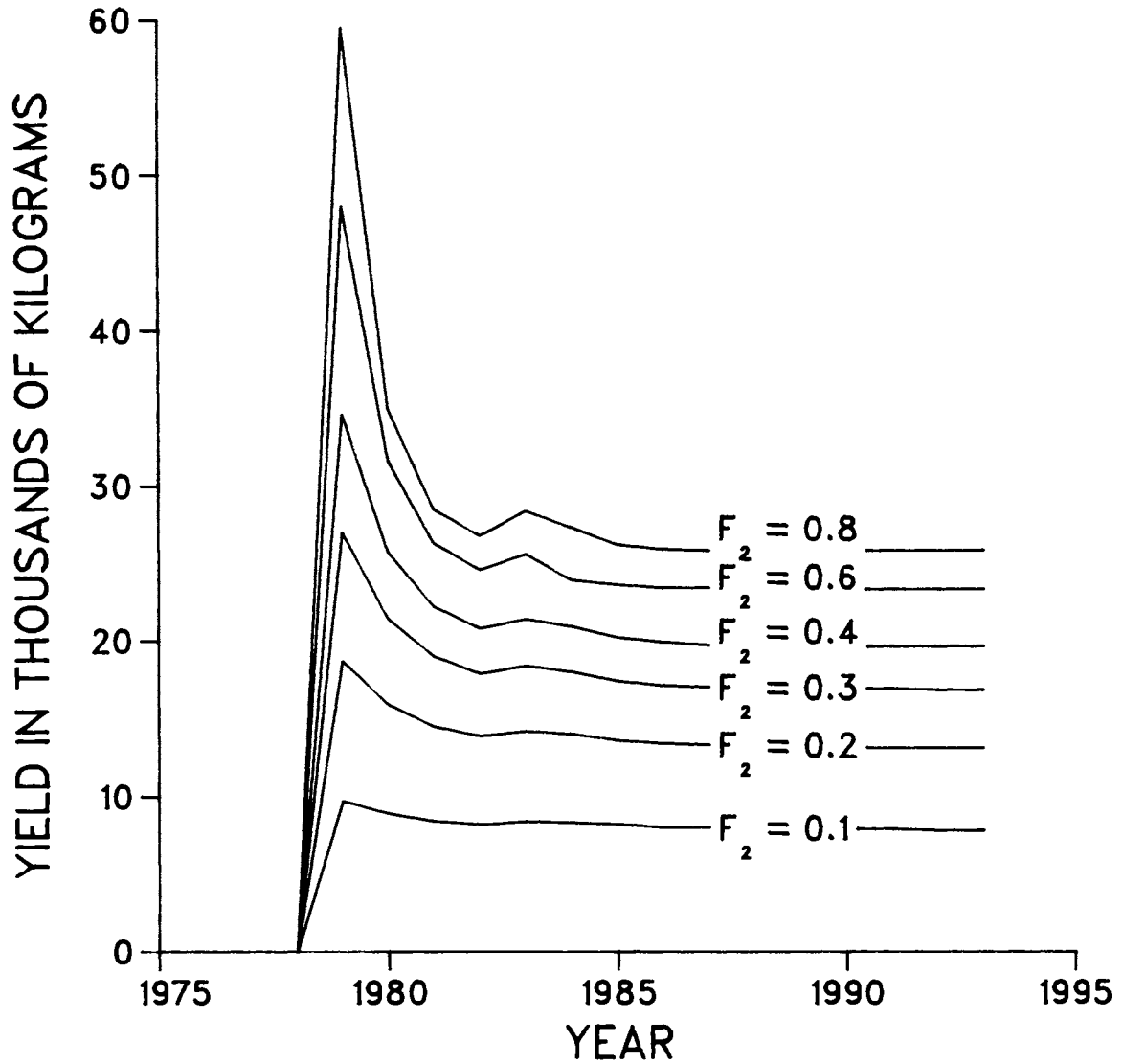


Figure 6.--Annual yield in weight of lake trout for the commercial fishery predicted for various levels of fishing (F_2). Fishing mortality rate for the sport fishery (F_1) was maintained at 0.22 in all cases.

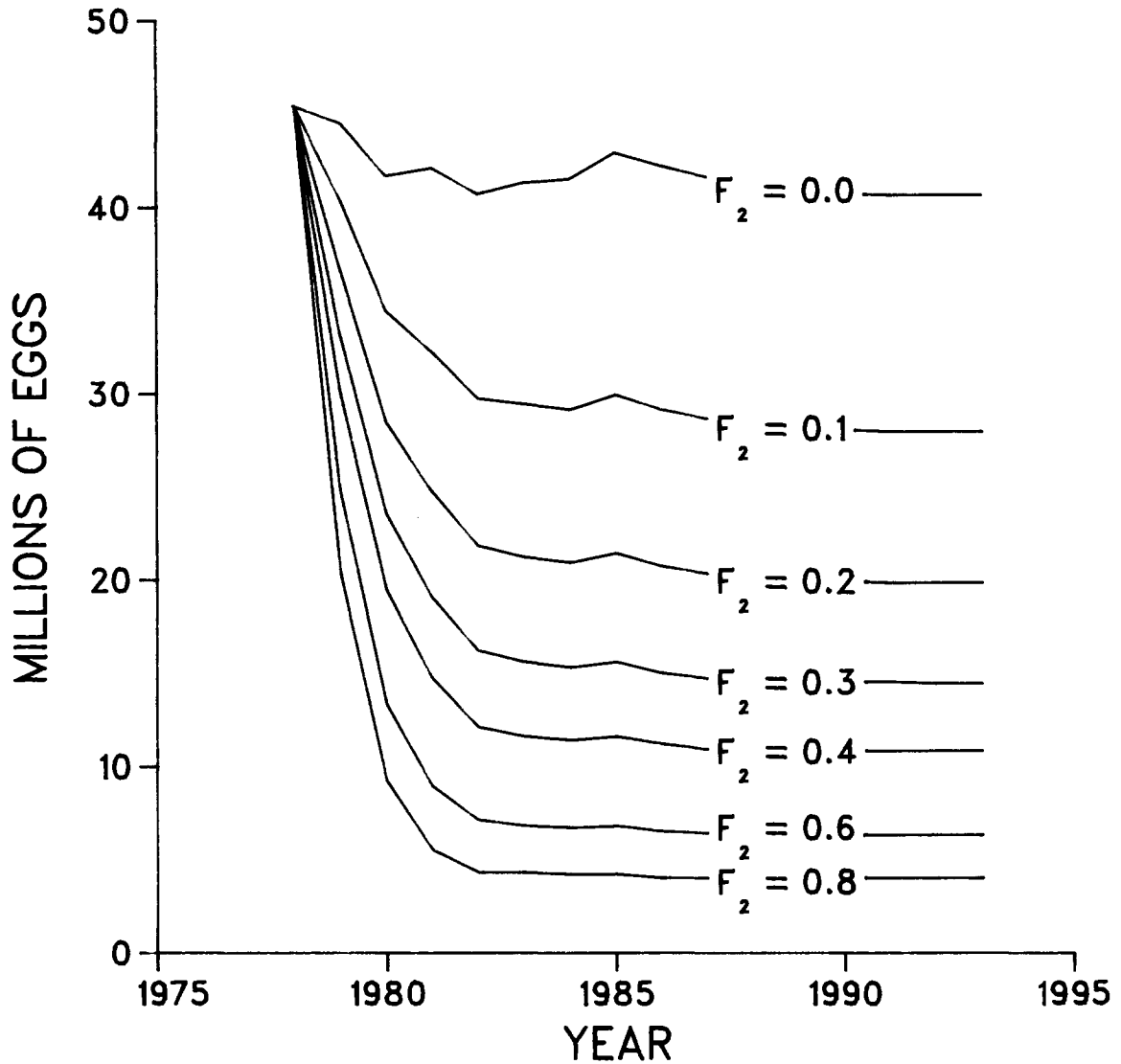


Figure 7.--Annual egg production of lake trout predicted for various levels of fishing mortality. Fishing mortality rate for the sport fishery (F_1) was maintained at 0.22 in all cases, while fishing mortality rate for the commercial fishery (F_2) varied as indicated.

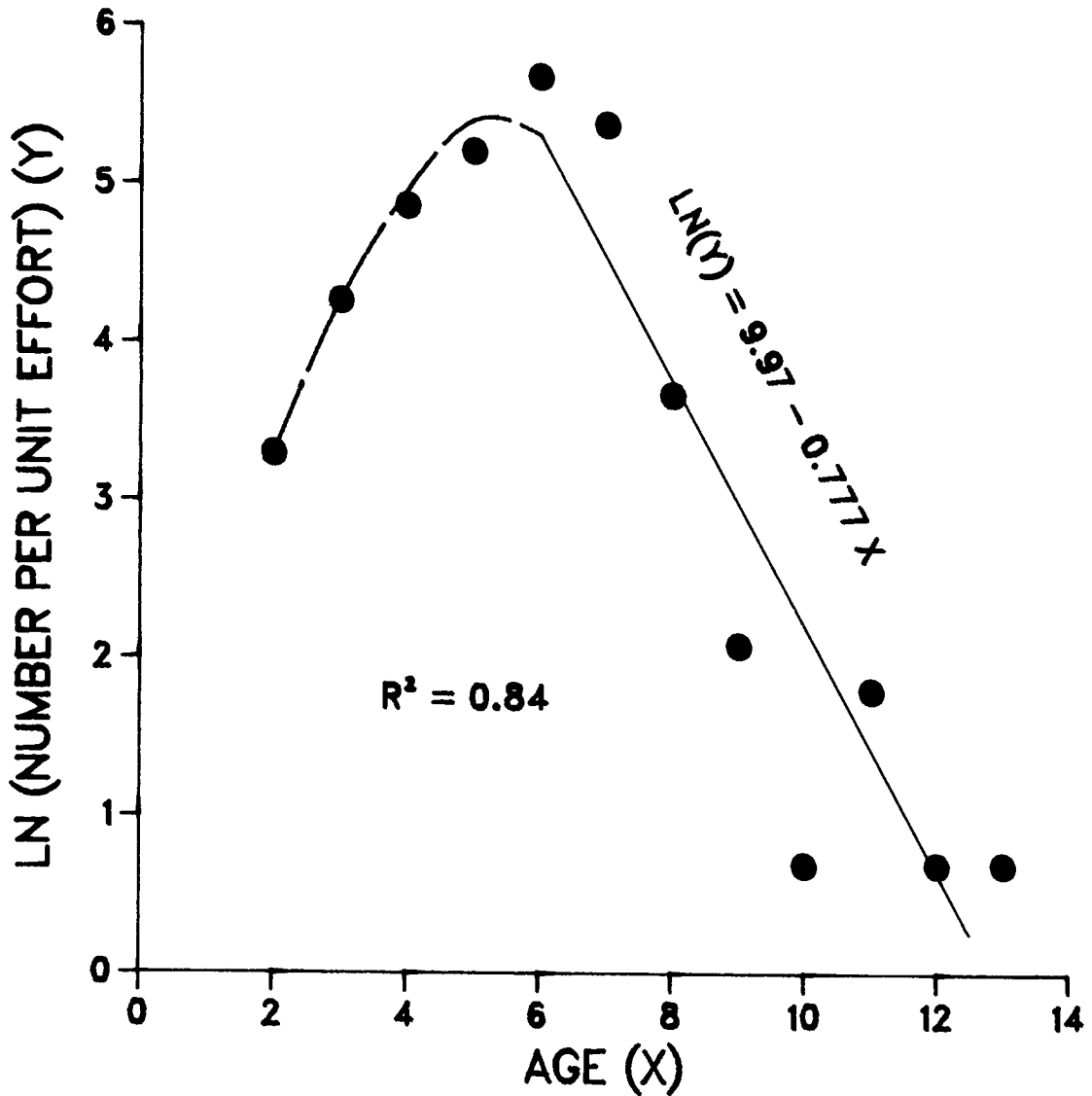


Figure 8.--Catch curve for lake trout collected during fall gill net sampling, 1978 to 1981. Cumulative effort was 22,200 meters of graded, experimental gill net fished for 24 hours. Regression was computed using fish from ages 6 to 13. The slope, 0.777, is an estimate of total instantaneous mortality rate (Z).

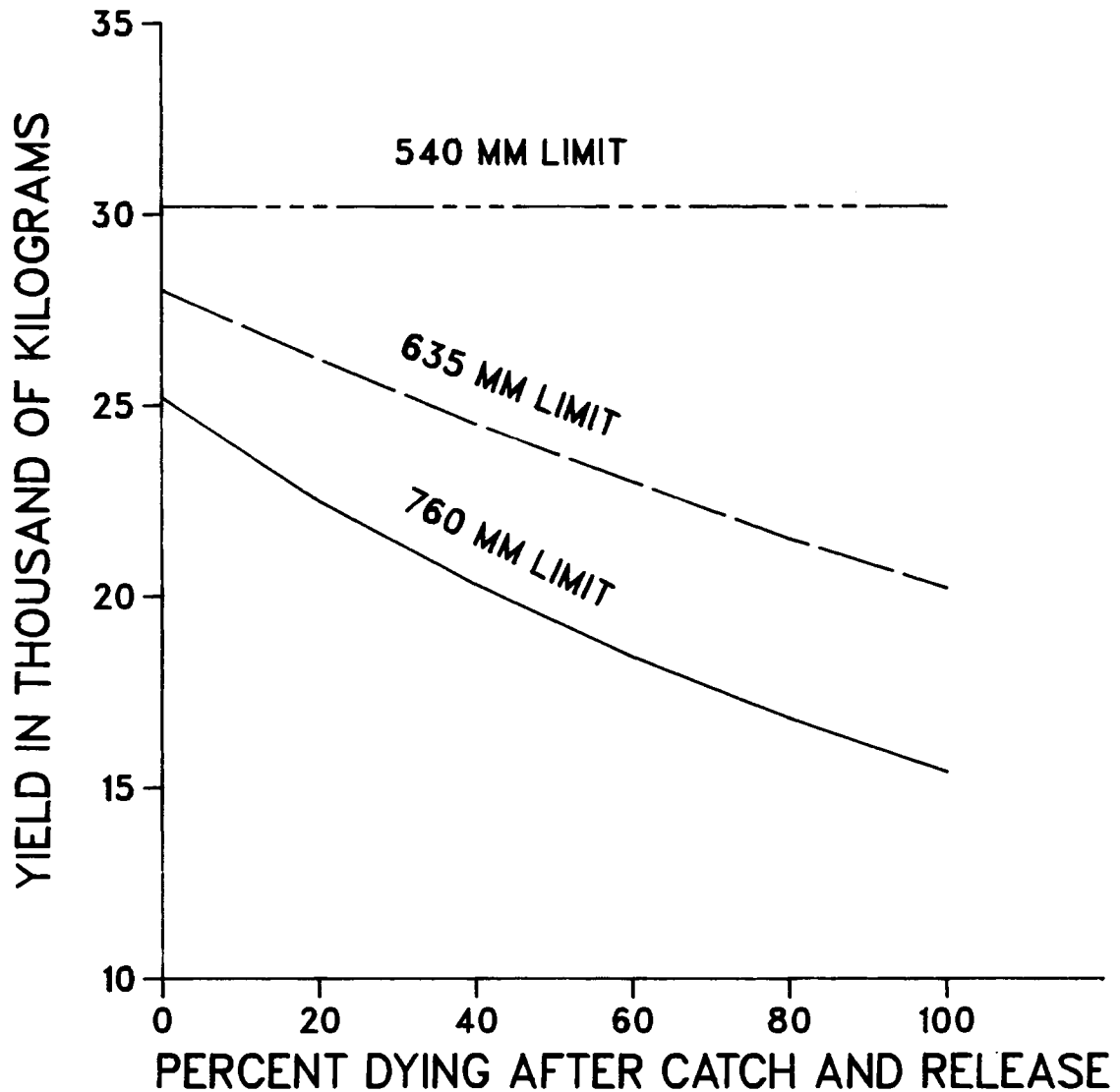


Figure 9.--The effect of different levels of hooking mortality from sport fishing on the total yield of lake trout (sport plus commercial) for 635 mm and 760 mm size limits applied only to sport fishery. A size limit (540 mm) where no hooking mortality occurs is shown for comparison.

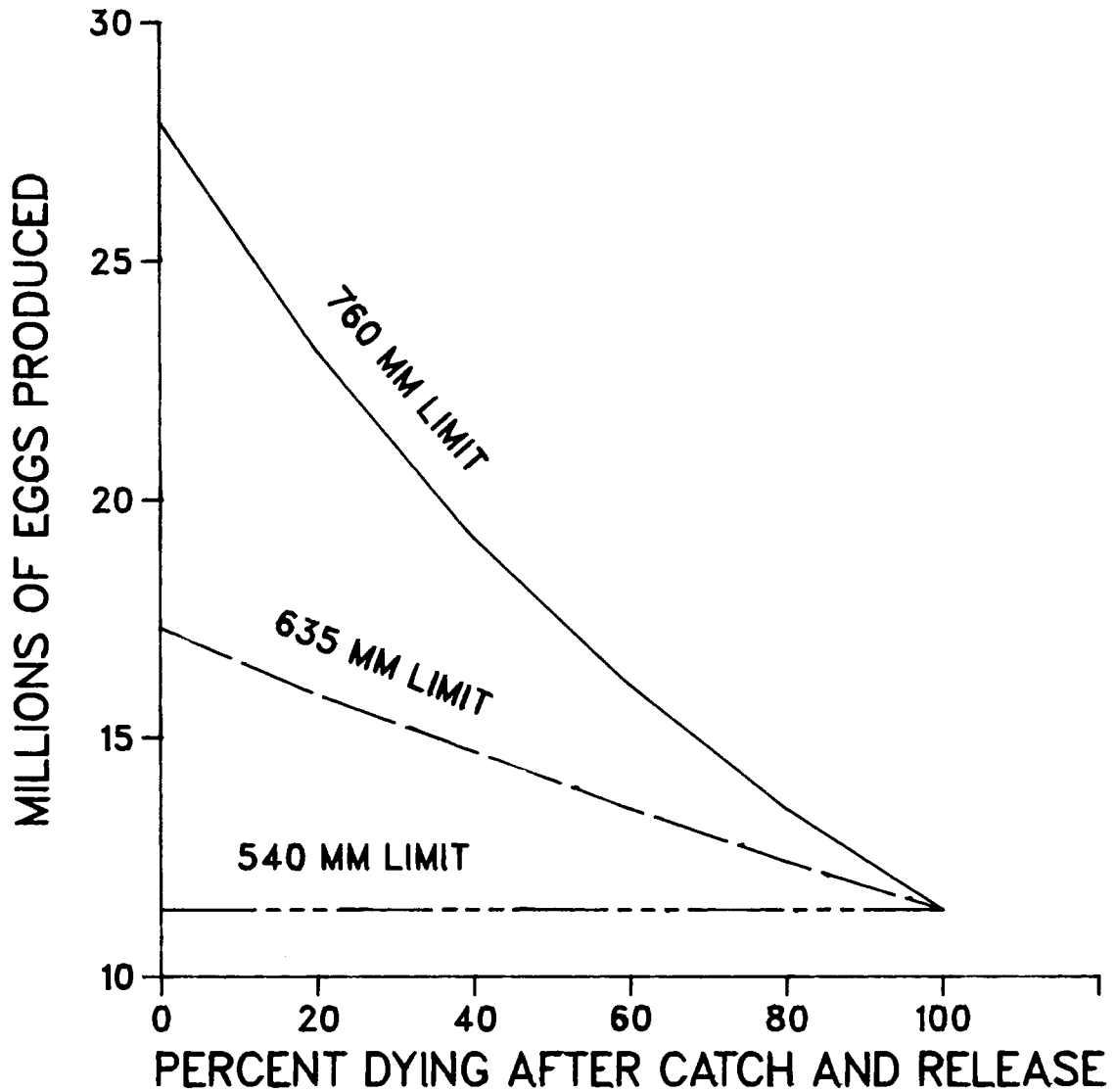


Figure 10.--The effect of different levels of hooking mortality from sport fishing on lake trout egg production for 635 mm and 760 mm size limits applied only to sport fishery. A size limit (540 mm) where no hooking mortality occurs is shown for comparison.

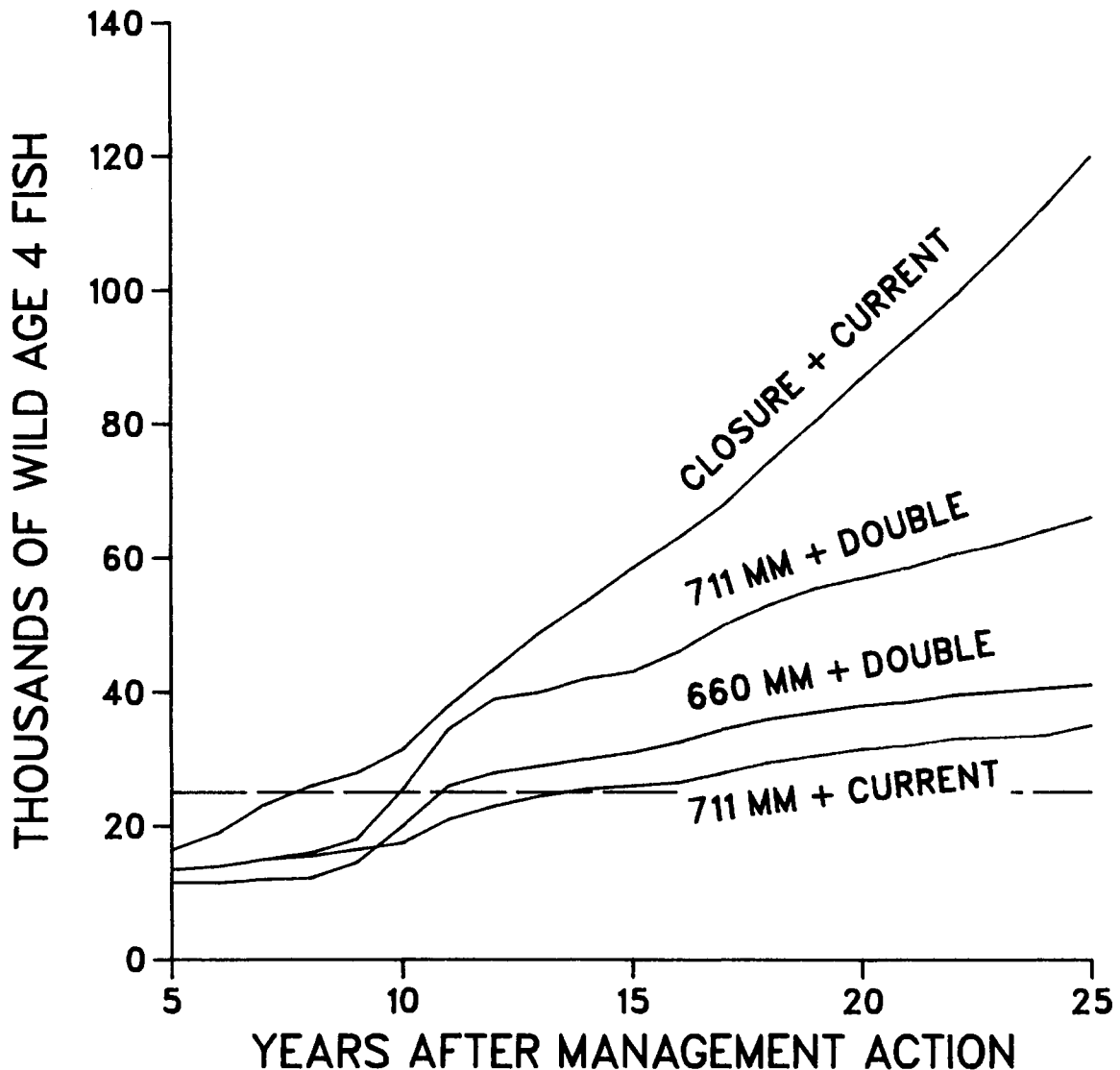


Figure 11.--Simulated production of wild lake trout of age 4 under four management schemes and a first year survival rate of 0.01. CLOSURE + CURRENT is the scheme of closing both fisheries and maintaining current stocking rates; 711 MM + DOUBLE is imposing a 711 mm size limit and doubling stocking rates; 660 MM + DOUBLE is imposing a 660 mm size limit and doubling stocking rates; and 711 MM + CURRENT is imposing a 711 mm size limit and maintaining current stocking rates. The dashed line represents the number of wild fish chosen as the criterion for achieving rehabilitation.

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Report approved by W. C. Latta.

Typed by G. M. Zurek

Appendix A. Solutions to differential equations describing change in number and catch from a cohort.

The equations were solved for each age interval separately. First, consider the interval from age 1 to age $x_{r,1}$. The general solution of equation (4) of text is:

$$N(x) = N(1) \text{ EXP}[-M(x-1)], \quad 1 \leq x < x_{r,1},$$

where in our model $N(1)$ was the number of yearlings planted and the other variables were defined in the text. Thus, it follows that,

$$N(x_{r,1}) = N(1) \text{ EXP}[-M(x_{r,1}-1)]$$

where $N(x_{r,1})$ is the number of fish surviving to age $x_{r,1}$.

For the interval from age $x_{r,1}$ to age $x_{r,2}$, the general solution is:

$$N(x) = N(x_{r,1}) \text{ EXP}[-(M+H_1)(x-x_{r,1})], \quad x_{r,1} \leq x < x_{r,2}$$

so we can calculate the number of fish surviving to age $x_{r,2}$ as:

$$N(x_{r,2}) = N(x_{r,1}) \text{ EXP}[-(M+H_1)(x_{r,2}-x_{r,1})]$$

Likewise, we can compute the decline in numbers for each successive interval, such that,

$$N(x_{c,1}) = N(x_{r,2}) \text{ EXP}[-(M+H_1+H_2)(x_{c,1}-x_{r,2})],$$

$$N(x_{c,2}) = N(x_{c,1}) \text{ EXP}[-(M+F_1+H_2)(x_{c,2}-x_{c,1})],$$

and finally,

$$N(x) = N(x_{c,2}) \text{ EXP}[-(M+F_1+F_2) (x-x_{c,2})],$$

where $N(x)$ is the number of fish present at any age older than age $x_{c,2}$.

When computing the catch, any age interval for which mortality is different must be treated separately. In our example, the catch for the first fishery (C_1) spans two intervals with different mortality, namely $x_{c,1} \leq x < x_{c,2}$ and $x_{c,2} \leq x$. Mortality in the first interval is $M+F_1+H_2$, because the second fishery is catching and releasing fish below age $x_{c,2}$ but not harvesting them. Mortality in the second interval is $M+F_1+F_2$, because both fisheries are harvesting fish above age $x_{c,2}$. Therefore, the total catch (C_1) for the first fishery is the sum of its catches in each of these intervals, where the catch in the first interval is:

$$dC_1/dx = F_1 N \quad x_{c,1} \leq x < x_{c,2}$$

$$C_1 = F_1 \cdot \{N(x_{c,1}) / (x_{c,2} - x_{c,1})\} \{1 - \text{EXP}[-(M+F_1+H_2) \cdot (x_{c,2} - x_{c,1})]\} / (M+F_1+H_2)$$

and the catch in the second interval is:

$$dC_1/dx = F_1 N \quad x_{c,2} \leq x$$

$$C_1 = F_1 \cdot \{N(x_{c,2})/(x-x_{c,2})\} \{1-\text{EXP}[-(M+F_1+F_2) \cdot (x_z-x_{c,2})]\}/(M+F_1+F_2)$$

where x_z is the maximum age attained, and the differential equations were solved in a manner similar to that of a standard Baranov catch equation (Ricker 1975).

The catch for the second fishery in our example occurs in an age interval ($x_{c,2} \leq x$) where mortality is uniform. Thus, the catch can be computed directly as:

$$C_2 = F_2 \{N(x_{c,2})/(x-x_{c,2})\} \{1-\text{EXP}[-(M+F_1+F_2) \cdot (x_z-x_{c,2})]\}/(M+F_1+F_2)$$

Derivations of equations for the numbers of sublegal fish caught and released are analogous to derivations of equations of harvested catch. The results for our example are:

$$J_1 = F_1 \{ \{N(x_{r,1})/(x_{r,2}-x_{r,1})\} \{1-\text{EXP}[-(M+H_1) \cdot (x_{r,2}-x_{r,1})]\}/(M+H_1) \\ + F_1 \{N(x_{r,2})/(x_{c,1}-x_{r,2})\} \{1-\text{EXP}[-(M+H_1+H_2) \cdot (x_{c,1}-x_{r,2})]\}/(M+H_1+H_2) \}$$

and,

$$\begin{aligned}
 J_2 = & F_2 \left(\left\{ \frac{N(x_{r,2})}{(x_{c,1} - x_{r,2})} \right\} \{1 - \text{EXP}[-(M + H_1 + H_2) \right. \\
 & \left. \cdot (x_{c,1} - x_{r,2})]\} / (M + H_1 + H_2) \right) \\
 & + F_2 \left\{ \frac{N(x_{c,1})}{(x_{c,2} - x_{c,1})} \right\} \{1 - \text{EXP}[-(M + F_1 + H_2) \\
 & \left. \cdot (x_{c,2} - x_{c,1})]\} / (M + F_1 + H_2) \right)
 \end{aligned}$$

Appendix B. Method of computing yield in weight of harvest.

The calculations for each cohort were first broken into the age intervals described in Appendix A, and then within these intervals, the calculations were divided further into intervals corresponding to integer ages i ($i = 1, 2, 3, \dots$). Thus, when all cohorts are considered, the model has a structure which is similar to that of a matrix model. The main difference is that the ages of first vulnerability ($x_{r,1}$ and $x_{r,2}$) and ages of entry into exploitation ($x_{c,1}$ and $x_{c,2}$) are usually not integers, and this makes the model a little more complicated. For the sake of illustration, consider the following age group i as fully recruited into the exploited stock and ignore the fact that there is more than one fishery operating. Then, yield in weight can be calculated by the following procedure:

- (1) Calculate the catch of age- i fish as,

$$C_i = F \cdot N_i [1 - \text{EXP}(-M-F)] / (F+M)$$

- (2) Calculate the approximate mean length (\bar{L}) of an age- i fish as it grows over the interval from age i to age $i+1$ by evaluating the von Bertalanffy growth equation at age $i+0.5$:

$$\bar{L} = L_{\infty} \{1 - \text{EXP}[-K(i+0.5 - x_0)]\}$$

Where L_{∞} , K , and x_0 are the parameters of the von Bertalanffy equation. Here, the assumption was

made that the age $i+0.5$ approximates the exact age corresponding to the mean length in the interval i to $i+1$. We checked the accuracy of this approximation by calculating the exact mean length for several age groups of lake trout. This can be done by evaluating the integral of the von Bertalanffy equation over the interval i to $i+1$ and then dividing the result (which is the area under the curve) by the base (which is unity). We found that the approximation was accurate to the nearest millimeter for fish over age 3 and deviated by only two millimeters for younger fish. Thus, the error caused by this mathematical approximation was trivial.

- (3) Calculate the approximate mean weight (\bar{W}) of an age- i fish by using a standard length-weight regression equation.

$$\bar{W} = \text{EXP}(A + B \ln(\bar{L}))$$

where A and B are the coefficients of the length-weight regression.

- (4) Calculate yield in weight of age- i fish as:

$$Y_i = C_1 \bar{W}$$

This procedure is repeated for all the age groups in the exploited stock, and the total yield is the sum of the yields over the age groups.