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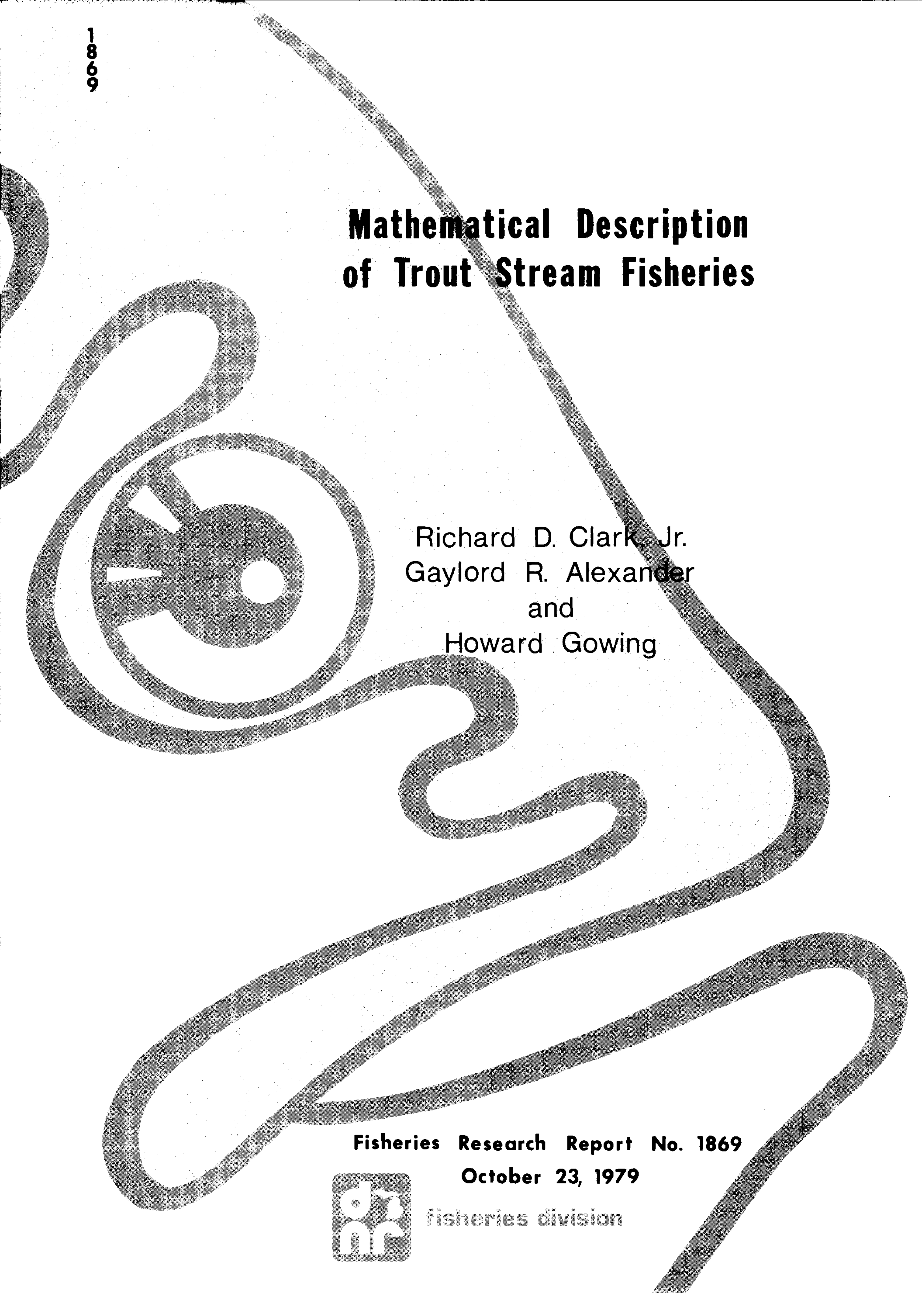

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MATHEMATICAL DESCRIPTION OF TROUT STREAM FISHERIES[1]

By Richard D. Clark, Jr., Gaylord R. Alexander, and
Howard Gowing

Abstract

A mathematical model of trout stream fisheries was developed which can be used to evaluate a variety of fishing regulations.

Density-dependent mortality was found in the first 2 years of life for each of the two brook trout and three brown trout populations studied. Regression equations were used to describe the density-dependent relationships for modeling purposes.

Equations were developed which used mortality, growth, and length-frequency information to calculate the number of fish in a population, number caught and harvested, number caught and released, number of deaths due to hooking mortality, number of natural deaths, and number recruiting for any time period and age group. Also, by adding a length-weight regression relationship, equations were developed for calculating yield in weight harvested, yield in weight caught and released, and gross biomass production for any time period and age group.

Effects of imposing different types of length limits, including minimum, inverted, or slot limits, can be analyzed with this mathematical technique. Fishing mortality and hooking mortality can be adjusted to simulate values typical for different gear types (e.g., artificial flies or live bait). Also, consequences of seasonal fluctuations in growth and fishing mortality can be assessed, including shifts in fishing season length or time frame.

The equations were incorporated into a computer simulator, TROUT.DYNAMICS. The brown trout fishery of the Main Au Sable River was simulated for a period in the past and a period in the future, to demonstrate application of the model.

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[1] Contribution from Dingell-Johnson Project F-35-R, Michigan.

Introduction

"Quality fishing regulations" have been tried on many trout streams with the broad purpose of improving fishing. They include the use of gear restrictions (e.g., artificial flies only), higher minimum size limits, and/or reduced daily creel limits. More recently inverted size limits (i.e., only permitting harvest of fish below a specified length), slot size limits (i.e., requiring release or permitting harvest of fish between two specified lengths), and catch and release regulations (i.e., prohibiting any harvest of fish) have been tested. Studies have shown that many of the problems surrounding "quality fishing regulations" are of a sociological nature (Shetter and Alexander 1962; Hunt 1970; Latta 1973), but the underlying biology should not be ignored. The biological consequences of imposing such complex regulations are difficult to evaluate, and problems often arise when biologists cannot give specific, biological reasons why one set of regulations is preferable to another.

In this report, a mathematical model for evaluating the biological aspects of trout fishing regulations is developed. The model is used to analyze a variety of fishing regulations for the brown trout fishery of the Main Au Sable River, Michigan.

Description of data base and study areas

Field studies conducted by several investigators to evaluate different fishing regulations have produced excellent data for several Michigan trout streams. Clark, Alexander, and Gowing (1979) gave a historical account of these studies. These are among the most detailed and complete fisheries data in existence, which is due in part to the relative ease of making abundance and catch estimates in trout streams as compared to fisheries in larger bodies of water. However, much credit must be given to the foresight, effort, and persistence of those who conducted these long-term evaluations.

Data used to develop the model came from three different trout streams located in the northcentral part of Michigan's lower peninsula-- Hunt Creek in Montmorency County, the North Branch of the Au Sable River in Otsego and Crawford counties, and Gamble Creek in Ogemaw County.

The study area on Hunt Creek supported only brook trout (*Salvelinus fontinalis*), Gamble Creek supported only brown trout (*Salmo trutta*), and the North Branch of the Au Sable River supported both brook and brown trout. All three streams are relatively stable environments for trout populations.

Data from these streams include: (1) semiannual estimates of trout abundance (before and after fishing season) in different size and age categories; (2) estimates of catch by age category; and (3) analyses of growth, condition, fecundity, and sexual maturity. Also, Hunt Creek brook trout and Gamble Creek brown trout populations have been monitored through years in which fishing was permitted (1945-65 on Hunt Creek, 1961-65 on Gamble Creek), as well as through years in which fishing was prohibited (1966-79 on Hunt Creek and 1966-73 on Gamble Creek). The fishery on the North Branch of the Au Sable River has been monitored from 1960-67 and 1971-79. More detailed descriptions of these fisheries and the data collection procedures are given by McFadden, Alexander, and Gowing (1967), Shetter (1969), Gowing (1975), Alexander and Ryckman (1976), Alexander (1977), and Alexander, Buc, and Schnicke (1979).

Theoretical basis for model

The basic modeling approach was to describe the processes of growth, mortality, and recruitment and the relationships between them. The underlying theme for development of the model was the theory that territoriality and predation regulate population size of trout in streams. These forces are responsible for density dependent birth and survival rates and relatively constant growth rates. Much scientific literature is available to support the theory of territoriality in stream salmonids (Kalleberg 1958; Chapman 1962, 1965, 1966; Allen 1969; McFadden 1969; Mason and Chapman 1965; and Le Cren 1965). Also, Alexander (1977a, 1977b) demonstrated that most natural mortality (at least of trout larger than young-of-year) in Michigan trout streams is from predation by large brown trout, birds (e.g., mergansers, kingfishers, and herons), and mammals (e.g., mink, otters, and raccoons).

Mortality

The model was developed around the assumption that legal-size and illegal-size trout (as defined by size limit regulations) are caught at the same rate. Experienced trout fishermen may balk at this assumption, since popular belief is that older, larger trout are wiser and more difficult to catch than smaller trout. Perhaps this is true for extremely large, old individuals, but data presented by Cooper, Shetter, and Hayne (1959, 1960) indicated trout of different sizes (and ages implicitly) were caught at rates roughly proportional to their abundance (Table 1).

Growth

Annual growth rate was considered constant for modeling purposes, because changes in regulations and other management activities which have significantly changed population densities have not significantly affected growth rates of trout in natural stream settings (McFadden 1969; Le Cren 1965; Cooper 1949; Saunders and Smith 1962; McFadden and Cooper 1964).

Le Cren (1965) suggested that salmonid populations in streams may not be limited in number by the food supply, but instead by density dependent movement and mortality mechanisms acting in response to the physical configuration of the stream. The term "movement" is used here in reference to both upstream and downstream roving or wandering of individual fish. Presumably, one of the causes of this movement is density, and we assume trout usually move from areas of high density to areas of low density. If each fish in a population is able to find and defend a favorable territory (i.e., one that provides it with enough cover to avoid predators and enough food for sustenance), then movements and predation are probably minimal. When population size exceeds the number of favorable territories, movement and predation seem to be effective in removing excess fish. The effectiveness of the regulatory mechanism appears to maintain the stability of growth in trout stream populations.

However, growth rates have been shown to be density dependent in some streams. Both Le Cren (1973) and Mortensen (1977a, 1977b) found inverse relationships between growth and density in brown trout streams. But Le Cren's experiments were conducted in stream sections blocked by screens which prevented movement, and in his description of the study area he seemed to imply that few natural predators were present. Mortensen worked on an extremely small stream with a mean width of less than 1 m and a total length of only 850 m. This stream was blocked upstream by a waterfall and downstream by Baaring vig (saltwater). Trout movement would be limited in such a stream. Mortensen provided no information on predation. The density dependent growth relationship found by these two authors rarely manifests itself in the trout of Michigan streams.

Another important consideration concerning trout growth is the possibility that growth rates may change over long periods of time. Cooper (1952) demonstrated that fishing was selective in cropping the larger individuals in a cohort of trout. If these cropped individuals were genetically superior with respect to growth, one might expect fishing to cause a decrease in the growth potential of trout in the population over time. Favro, Kuo, and McDonald (1979) suggested that a decline in growth rate found for Au Sable River brown trout may be linked to such a selection process. But, with few exceptions, growth rates of trout in streams have remained remarkably constant over long periods, even in heavily exploited stocks (McFadden 1961, 1969; McFadden et al 1967; Cooper 1949).

While growth from year to year appears to remain relatively constant, growth rates do fluctuate throughout each annual cycle (Cooper 1953). This is a result of seasonal changes in the amount of food eaten by trout as it relates to food abundance, food availability, and water temperature. Seasonal periodicity of growth is important to consider when simulating a trout population, because it has a direct effect on recruitment rates.

Recruitment

Number of trout recruiting into a fishery depends on number of young produced and survival of those young over the period required to grow to the minimum size limit. Total egg production of a trout population can be estimated by:

$$\text{Eggs} = \sum_{i=1}^{x} \sum_{j=1}^{y} (\text{FEM}_{ij})(\text{FMAT}_{ij})(\text{EC}_j)$$

Eggs = total egg production

x = number of age groups

y = number of length (inch) groups

FEM_{ij} = number of females in each length-age group as calculated above

FMAT_{ij} = percent females mature in each length-age group

EC = mean egg content of females in each length category

Necessary data were available to estimate egg production for 22 years for brook trout in Hunt Creek (14 years from McFadden et al. 1967, plus 8 years unpublished data from Hunt Creek Trout Research Station) and for 8 years for brook and brown trout in the North Branch of the Au Sable River (Shetter 1969; Alexander 1974). Also, fecundity data from the Platte River (Taube 1976) were applied to brown trout population data from Gamble Creek (Gowing 1975), to estimate egg production for 7 years in Gamble Creek. Numbers of trout eggs produced in Hunt Creek and numbers of age-0 trout which survived from the brood a year later are presented in Table 2. When numbers of eggs are plotted against their ensuing survival rates (Fig. 1), it becomes apparent that first-year survival is density dependent. A regression equation was employed to describe this relationship:

$$S = a + b \cdot \ln\left(\frac{\text{eggs}}{1000}\right)$$

S = survival rate of eggs to age 0 (next fall)

a = intercept of regression line

b = slope of regression line

eggs = total egg production

Egg to age-0 survivorship for brook and brown trout from the North Branch of the Au Sable (Shetter 1969) and brown trout from Gamble Creek (Gowing 1975) are presented in Tables 3, 4, and 5, respectively. Regression results were significant at $P < 0.10$ for each population, except for browns in the North Branch which were significant at $P = 0.17$. These regressions had the following R^2 values: brook trout, Hunt Creek ($R^2 = 0.57$); brook trout, North Branch, upper section ($R^2 = 0.87$); brown trout, North Branch, upper section ($R^2 = 0.41$); brown trout, Gamble Creek ($R^2 = 0.62$).

Trout in Michigan streams do not grow fast enough to enter the catch in their first year of life. Even in a fast growing population with a minimum limit of 152 mm (6 inches), trout would not enter the catch until their second summer, and it could be two or more growing seasons before the slower growing individuals in a cohort reached legal size. Obviously, several years of survivorship beyond the first year must be addressed if recruitment is to be represented with realism. McFadden et al. (1967) showed that survival in second, as well as first, year of life was density dependent in Hunt Creek (Table 2). A regression equation was also employed to calculate the relationship between numbers and second-year survival rate for Hunt Creek ($P = 0.01$, $R^2 = 0.54$). Survival in the second year was also density dependent for brook and brown trout in other streams (Tables 3, 4, and 5). Regression relationships between numbers and survival rate were statistically significant ($P = 0.05$) for: brook trout, North Branch, upper section ($R^2 = 0.80$); brown trout, North Branch, upper section ($R^2 = 0.81$); brown trout, Gamble Creek ($R^2 = 0.79$). No significant relationship was found between numbers and survival of trout older than age I; thus a constant mean rate was used to represent survival in third and subsequent years of life in developing the model.

Mathematical development of model

Mortality

In most fisheries models, two major sources of mortality are considered, natural and fishing. The relationship between the two can be expressed by the equation from Ricker (1975):

$$A = m + n - mn \qquad (1)$$

A = total mortality rate for some time period

n = conditional, natural mortality rate

m = conditional, fishing mortality rate

In a recreational trout fishery, we want to address a third source of mortality, namely hooking mortality of fish caught and released. We can add hooking mortality to equation (1) in the following fashion:

$$A = m + n + mh - mn - mhn \qquad (2)$$

where h is defined as the probability of a fish dying after being caught and released.

Applying this idea to a simple minimum size limit regulation, we can calculate the total mortality of an age group as:

$$A = n + \frac{L}{N}m + \frac{I}{N}mh - \frac{L}{N}mn - \frac{I}{N}mhn \qquad (3)$$

N = total number in cohort at beginning of time period

L = number of legal-size fish in cohort

I = number of illegal-size fish in cohort

This equation assumes all illegal-size fish caught are released and all legal-size fish caught are harvested. Notice that the proportion L/N represents the fraction of the cohort subjected to harvest, while I/N represents the fraction subjected to hooking mortality. When L/N is multiplied by m it reduces the amount of fishing mortality going into the total mortality calculation in proportion to the numbers of fish subject to harvest. Likewise, the term Imh/N reduces the effect of hooking mortality on total mortality. Note also that the interaction term between fishing and natural mortalities (mn), applies only to the L/N portion of the cohort, while the interaction term between hooking and natural mortalities (mhn) applies only to the I/N portion.

By adding a time dimension (t) to our model and referring to Ricker (1975) we find:

$$N_{t+1} = N_t - N_t A_t \tag{4}$$

and since N_t was defined as:

$$N_t = L_t + I_t \tag{5}$$

the following model can be developed for describing changes in numbers from one time period to the next by combining equations (3), (4), and (5) and reducing:

$$N_{t+1} = N_t - N_t n_t - L_t m_t - I_t m_t h + L_t m_t n_t + I_t n_t m_t h \tag{6}$$

Note that h has no time dimension, since it will be assumed constant over time.

This mortality model can easily be expanded to accommodate a more complicated division of the cohort, such as one that would develop if a slot size limit regulation were imposed. For example, the regulation currently being tested on the Main Stream of the Au Sable River in Crawford County, Michigan, allows harvest of trout between 203 mm and 305 mm and of trout 406 mm or larger. Such a regulation necessitates the rather complicated breakdown of a cohort depicted in Figure 2.

Fish in cross-hatched areas T and V (Fig. 2) are of legal size, and fish in areas R and U are of illegal size. Thus, the total number of fish in the cohort (N_t) can be represented as:

$$N_t = R_t + T_t + U_t + V_t \tag{7}$$

Taking equation (7) and following our earlier logic, the mortality model for slot limit regulations becomes:

$$\begin{aligned} N_{t+1} = {} & N_t - N_t n_t - R_t m_t h - T_t m_t - U_t m_t h - V_t m_t \\ & + R_t n_t m_t h + T_t n_t m_t + U_t n_t m_t h + V_t n_t m_t \end{aligned} \tag{8}$$

Another useful expression for N_{t+1} is:

$$N_{t+1} = N_t - C_t - D_t - H_t \tag{9}$$

C = number of fish harvested in time "t"

D = number of fish dying natural deaths

H = number of deaths due to hooking mortality

After comparison of equations (8) and (9), it becomes apparent that we can express the different sources of death from equation (9) by using the terms from equation (8). That is, the legal catch can be calculated as,

$$C_t = T_t m + V_t m_t - \frac{T_t m_t n_t}{2} - \frac{V_t m_t n_t}{2} \tag{10}$$

and natural deaths as,

$$D_t = N_t n_t - \frac{R_t n_t m_t h}{2} - \frac{T_t n_t m_t}{2} - \frac{U_t n_t m_t h}{2} - \frac{V_t n_t m_t}{2} \qquad (11)$$

and deaths due to hooking as,

$$H_t = R_t m_t h + U_t m_t h - \frac{R_t n_t m_t h}{2} - \frac{U_t n_t m_t h}{2} \qquad (12)$$

Another quantity of interest, numbers of fish caught and released (J_t), can be calculated as,

$$J_t = R_t m_t + U_t m_t - R_t n_t m_t h - U_t n_t m_t h \qquad (13)$$

Growth and recruitment

The Weibull probability density function (PDF) is a flexible equation which can be used to approximate almost any unimodal probability distribution (Clark and Lackey 1975). We assumed that the length frequency distribution of a trout cohort can be approximated by a three parameter Weibull PDF of the form:

$$f(x) = \frac{p}{q^p} (x-k)^{p-1} e^{-[(x-k)/q]^p} \qquad (14)$$

$x \geq k$

$p \geq 0$

where:

x = random variable (length)

p = shape parameter

q = scale parameter

k = constant

The cumulative distribution function is:

$$g(x') = \int_0^{x'} f(x')dx = 1 - e^{-[(x'-k)/q]^p} \qquad (15)$$

From the definition of a cumulative distribution function, it follows that a cohort with N members would have their lengths distributed such that the probability a fish has a length less than or equal to x' is represented by the expression g(x') .

Therefore, from Figure 2 and equation (15) we get:

$$R_t = N_t g(x_{2,t}) \qquad (16)$$

$$T_t = N_t[g(x_{3,t}) - g(x_{2,t})] \qquad (17)$$

$$U_t = N_t[g(x_{4,t}) - g(x_{3,t})] \qquad (18)$$

and because V_t can be described in terms of the complimentary cumulative distribution which is 1-g(x'), we get:

$$V_t = N_t[1-g(x_{4,t})] \qquad (19)$$

In order to simulate the behavior of a fishery it becomes necessary to place our description of a length frequency in the context of an entire population. As an example, consider the empirical data available for brook trout in Hunt Creek. Cooper (1953) gave data on seasonal growth periodicity and McFadden et al. (1967) gave length frequencies of each age group. From this information a three-dimensional figure was created which is itself a model of a trout population. One can see from inspecting Figure 3 that the population can be described as a series of length frequency distributions which are passing through time. The distributions are related to the "length dimension" according to the seasonal growth pattern and are related to the "number dimension" according to the mortality pattern.

To describe the seasonal growth pattern, the variable G_t was defined as the proportion of annual growth experienced in small time period, t. Thus,

$$\sum_{t=1}^{52} G_t = 1.0$$

where t equals 1 week, and since trout population estimates were conducted near the beginning of October on the streams we studied, October 1 was defined as t_o. Weibull distributions were fitted to length frequency distributions for each age group represented in field data by the technique described by Clark and Lackey (1975). This technique uses estimates of low, modal, and high values of a frequency distribution to estimate the Weibull parameters through an iterative process.

An age dimension was added to important lengths shown in Figure 2, and they were defined as follows:

$x_{1,t,i}$ = smallest length represented in length frequency of age i at time t

$x_{2,t,i}$ = first minimum size limit; does not change with time or age, and henceforth will be referred to as x_2

$x_{3,t,i}$ = maximum size limit; does not change with time or age, and henceforth will be referred to as x_3

$x_{4,t,i}$ = second minimum size limit; does not change with size or age and henceforth will be referred to as x_4

$x_{5,t,i}$ = longest length represented in length frequency of age i at time t

Also, if we define $x_{m,t,i}$ as the mode of the length frequency of age i at time t, we can calculate the Weibull parameters for a length frequency in any week of the year by calculating low, high, and modal values for the distributions as:

$$x_{1,t+1,i} = x_{1,t,i} + (G_t)(L_{i+1,t_o} - L_{i,t_o}) \tag{20}$$

$$x_{5,t+1,i} = x_{5,t,i} + (G_t)(L_{i+1,t_o} - L_{i,t_o}) \tag{21}$$

$$x_{m,t+1,i} = x_{m,t,i} + (G_t)(L_{i+1,t_o} - L_{i,t_o}) \tag{22}$$

If the resulting Weibull parameters are $k_{i,t}$, $q_{i,t}$, and $p_{i,t}$, then $R_{i,t}$ can be expressed as a combination of equations (15) and (16):

$$R_{i,t} = N_{i,t}(1 - e^{-\theta_2}) \tag{23}$$

where,

$$\theta_2 = [(x_2 - k_{i,t}) / q_{i,t}]^{p_{i,t}}$$

The other length categories were expressed in similar fashion: $T_{i,t}$ as a combination of equations (15) and (17);

$$T_{i,t} = N_{i,t}(e^{-\theta_2} - e^{-\theta_3}) \tag{24}$$

where,

$$\theta_3 = [(x_3 - k_{i,t}) / q_{i,t}]^{p_{i,t}}$$

$U_{i,t}$ as a combination of equations (15) and (18)

$$U_{i,t} = N_{i,t}(e^{-\theta_3} - e^{-\theta_4}) \tag{25}$$

where,

$$\theta_4 = [(x_4 - k_{i,t}) / q_{i,t}]^{p_{i,t}}$$

and finally, $V_{i,t}$ as a combination of equations (15) and (19):

$$V_{i,t} = N_{i,t}\, e^{-\theta_4} \qquad (26)$$

Combining mortality, growth, and recruitment

The dynamics of many interesting population processes and fishery outputs can be described as single equations by continuing with the logic we have developed.

Population numbers.--Changes in the number of fish in an age group over time was expressed by combining equations (8), (23), (24), (25), and (26) and reducing:

$$N_{i,t+1} = N_{i,t}\left\{(1-n_{i,t})(1-m_t h) + [m_t(h-1)(1-n_{i,t})(e^{-\theta_2} - e^{-\theta_3} + e^{-\theta_4})]\right\} \qquad (27)$$

Note that because m_t was assumed constant for all size and age groups, it does not need the i subscript.

Catch.--Harvested catch from an age group in time t was calculated by combining equations (10), (24), and (26) and reducing:

$$C_{i,t} = N_{i,t} m_t \left(1 - \frac{n_{i,t}}{2}\right)(e^{-\theta_2} - e^{-\theta_3} + e^{-\theta_4}) \qquad (28)$$

The equation for calculating number of fish caught and released $(J_{i,t})$ was developed using equations (13), (23), and (25):

$$J_{i,t} = N_{i,t} m_t (1 - n_{i,t} h)(1 - e^{-\theta_2} + e^{-\theta_3} - e^{-\theta_4}) \qquad (29)$$

Hooking deaths.--Number of fish dying due to hooking mortality was expressed as a combination of equations (12), (23), and (25):

$$H_{i,t} = N_{i,t}m_th(1 - \frac{n_{i,t}}{2})(1 - e^{-\theta_2} + e^{-\theta_3} - e^{-\theta_4}) \qquad (30)$$

Natural deaths.--Number of natural deaths was expressed as a combination of equations (11), (23), (24), (25), and (26):

$$D_{i,t} = N_{i,t}n_{i,t}[1 - \frac{1}{2}(1-h)(e^{-\theta_2} - e^{-\theta_3} + e^{-\theta_4})] \qquad (31)$$

Yield.--Deriving equations for yield in weight was more complicated. Length (x') and weight (w') were related by using the familiar regression equation:

$$\ell n(w') = \alpha + \beta \ell n(x') \qquad (32)$$

α = intercept

β = slope

Basically, the catch equation (28) represents the sum of the fish caught in two length intervals in the Weibull distribution (Fig. 2), the interval between x_2 and x_3 and the interval over x_4 (i.e., groups $T_{i,t}$ and $V_{i,t}$). Yield in weight from these intervals is:

$$Y_{i,t} = \bar{w}_T m_t T_{i,t} + \bar{w}_V m_t V_{i,t} - \frac{\bar{w}_T n_{i,t} m_t}{2} T_{i,t} - \frac{\bar{w}_V n_{i,t} m_t}{2} V_{i,t} \qquad (33)$$

where,

$\bar{w}_T$ = mean weight of a fish in interval $T_{i,t}$

$\bar{w}_V$ = mean weight of a fish in interval $V_{i,t}$

In order to calculate the mean weights $\bar{w}_T$ and $\bar{w}_V$, we first calculated the corresponding mean lengths $\bar{x}_T$ and $\bar{x}_V$, and then applied regression equation (32). Mean length in interval between x_2 and x_3 (the T interval) can be calculated as follows:

$$\bar{x}_T = k_{i,t} + q_{i,t}\left\{\ln[2/(e^{-\theta_2} + e^{-\theta_3})]\right\}^{1/p_{i,t}} \qquad (34)$$

also, mean length in V interval is:

$$\bar{x}_V = k_{i,t} + q_{i,t}[0.69315 + \theta_4]^{1/p_{i,t}} \qquad (35)$$

Substituting equations (34) and (35) into equation (32), then into equation (33), the following equation for harvested yield was obtained:

$$Y_{i,t} = N_{i,t}m_t(1 - \frac{n_{i,t}}{2})(e^{\gamma_1-\theta_2} - e^{\gamma_1-\theta_3} + e^{\gamma_2-\theta_4}) \qquad (36)$$

where:

$$\gamma_1 = \alpha + \beta\ln\left[k_{i,t} + q_{i,t}\left\{\ln[2/(e^{-\theta_2} + e^{-\theta_3})]\right\}^{1/p_{i,t}}\right]$$

and,

$$\gamma_2 = \alpha + \beta\ln\left[k_{i,t} + q_{i,t}[0.69315 + \theta_4]^{1/p_{i,t}}\right]$$

An equation for yield in weight of fish caught and released ($YJ_{i,t}$) was similarly derived:

$$YJ_{i,t} = N_{i,t}m_t(1 - n_{i,t}h)(e^{\gamma_3} - e^{\gamma_3-\theta_2} + e^{\gamma_4-\theta_4} - e^{\gamma_4-\theta_6}) \qquad (37)$$

where:

$$\gamma_3 = \alpha + \beta \ell n \left[k_{i,t} + q_{i,t} \left\{ \ell n[2/(1-e^{-\theta_2})] \right\}^{1/p_{i,t}} \right]$$

and

$$\gamma_4 = \alpha + \beta \ell n \left[k_{i,t} + q_{i,t} \left\{ \ell n[2/(e^{-\theta_3} - e^{-\theta_4})] \right\}^{1/p_{i,t}} \right]$$

Recruitment and discharge.--The processes of recruitment (growing into legal range) and discharge (growing out of legal range) can be studied with this model, because numbers recruiting and discharging can be calculated directly as functions of growth and mortality.

The increment of growth in length can be calculated for any time period, t . When this increment is subtracted from the first minimum size limit, x_2 , a length, x_r , is obtained:

$$x_r = x_2 - G_t(L_{i+1,t_o} - L_{i,t_o}) \qquad (38)$$

All fish with lengths between x_r and x_2 will recruit into the first legal range during week t if they survive the week. Thus, recruitment ($REC1_{i,t}$) can be calculated as the number of fish in the x_r to x_2 interval minus those dying:

$$REC1_{i,t} = N_{i,t}(1-m_t h)(1-n_{i,t})(e^{-\theta_r} - e^{-\theta_2}) \qquad (39)$$

where,

$$\theta_r = [(x_r - k_{i,t})/q_{i,t}]^{p_{i,t}}$$

Similarly, equations can be derived to calculate number discharging ($DIS_{i,t}$) and number recruiting into second legal range ($REC2_{i,t}$):

$$DIS_{i,t} = N_{i,t}(1-m_t h)(1-n_{i,t})(e^{-\theta_s} - e^{-\theta_3}) \tag{40}$$

and,

$$REC2_{i,t} = N_{i,t}(1-m_t h)(1-n_{i,t}) \tag{41}$$

where,

$$\theta_s = [(x_s - k_{i,t})/q_{i,t}]^{p_{i,t}}$$

$$x_s = x_3 - G_t(L_{i+1,t_o} - L_{i,t_o})$$

and,

$$\theta_v = [(x_v - k_{i,t})/q_{i,t}]^{p_{i,t}}$$

$$x_v = x_4 - G_t(L_{i+1,t_o} - L_{i,t_o})$$

Biomass production.--In a typical dynamic pool model (Ricker 1975; Beverton and Holt 1957), calculating biomass production is more or less meaningless, because recruitment is usually unknown and considered relative. However, a production equation would make sense in a model in which population numbers and recruitment are regulated by density-dependent mortality. To accomplish this form of population regulation, the regression equations presented earlier for predicting annual survival rates in the first 2 years of life were used in the model. These regression equations had the effect of density-dependent regulation, because their negative slopes produced high survival rates when numbers present were low and low survival rates when numbers present were high. In practice this caused simulated populations to seek an equilibrium state for a given set of regulations. If one assumes the parameters of the regression equations are defined by territoriality or competition for limited resources (e.g., energy or space), then biomass production can be a meaningful performance measure for the fishery.

Gross production ($P_{i,t}$), defined as the total increase in new biomass over time, was estimated for weekly time periods by:

$$P_{i,t} = W_{i,t}[N_{i,t} - (D_{i,t} + C_{i,t} + H_{i,t})/2] \qquad (42)$$

where $W_{i,t}$ is the mean weight increase of an individual of age i in week t and is calculated by applying length-weight regression (32) to growth in length.

Model application

Any model with equations as numerous and complex as the ones we developed for trout stream fisheries would be difficult, if not impossible, to apply to practical management problems without the aid of an electronic computer. Thus, we coded the equations in FORTRAN computer language in the form of a trout population simulator, named TROUT.DYNAMICS.

Description of population simulator

The simulator divides an annual cycle into weekly time periods (t) in which equations for $N_{i,t}$, $C_{i,t}$, $J_{i,t}$, $Y_{i,t}$, $YJ_{i,t}$, $H_{i,t}$, $D_{i,t}$, $REC1_{i,t}$, $DIS_{i,t}$, $REC2_{i,t}$, and $P_{i,t}$ are solved. Annual values are obtained by summing weekly values.

Annual natural mortality and growth are age specific. Natural mortality of age 0 and age 1 fish is calculated as a function of density using the regression equations. Natural mortality of age 2 and older fish is constant. The annual n_i's are spread over the weekly time periods in exponential fashion such that natural mortality occurs at a constant rate for all time periods t.

Annual growth increments for each age group are distributed over the weeks by using vector G_t which assigns each week with the percent of the annual growth observed by Cooper (1953).

The annual fishing rate (m) is specified by the investigator, as is the distribution of m over the weekly time periods. We distributed m in our experiments according to continuous creel census data from Hunt Creek, Michigan, from 1960 to 1965 (Williams et al. 1966, 1967; Alexander et al. 1964; and Alexander and Shetter 1961, 1962).

The simulator calculates parameters for Weibull distributions internally. It uses estimates of the low, modal, and high lengths of length-frequency distributions to calculate Weibull parameters.

While the simulator uses metric units of length and weight, it reproduces the population and catch in size categories which correspond to inch groups. Thus, model output can be directly compared to historical data which are in English units of measure.

Description of study fishery

TROUT.DYNAMICS was applied to the brown trout fishery of the Main Au Sable River, Crawford County, Michigan. The purpose was to illustrate the model's ability to examine a variety of regulations and biological outputs. The section of river chosen for the example starts at Burton's Landing, 9 km below the town of Grayling, and extends 14 km downstream to Wakeley Bridge. This section of the Au Sable is recognized as one of the best trout stream fisheries in Michigan, and contains populations of brown, brook, and rainbow trout. It has been regulated by various sets of "quality" regulations since the mid-1950's.

Data collection procedures and background information on this fishery were given by Alexander, Buc, and Schnicke (1979). Briefly, Michigan Department of Natural Resources personnel defined two fish sampling stations in the Burton-to-Wakeley section, each about 0.4 km long. Estimates of abundance by size and age group were made near October 1 at these stations from 1959-63 and 1971-78. Crews used dc electrofishing gear and mark-and-recapture methods to collect population data. Estimates of numbers of trout harvested were made by randomized creel census procedures (Alexander and Shetter 1967) from 1960-65 and in 1976. Population and creel census data were used to compute average numbers of trout per hectare in population and harvest, respectively. These averages were assumed to be representative of the entire stream segment.

Alexander et al. (1979) reported several significant changes in the Burton-To-Wakeley brown trout fishery from the early 1960's to the mid-1970's. They found a decrease in mean lengths of trout in each age group, an increase in survival rates of trout in age groups 1 and 2, a decrease in survival rates of trout in age groups 0 and 3, and a decrease in fishing pressure.

Causes for these changes could not be determined with certainty, because a number of events occurred during this period which might have affected the fishery. Fishing regulations were changed six times between 1955 and 1976. The State of Michigan phased out fish production, with its related waste discharge, at the Grayling Hatchery in the mid-60's. The city of Grayling stopped discharging sewage effluent into the Main Au Sable in 1971. As a result, nitrogen concentrations decreased in the Burton-to-Wakeley section by about 70% between 1971 and 1972, and phosphorus concentrations decreased by about 10% from 1966 to 1972 (Coopes et al. 1974). Such a loss of nutrients could have been responsible for the reduction in average sizes of trout in the mid-1970's, but other authors (Favro, Kuo, and McDonald 1979) have suggested that the growth potential of brown trout in this river section was reduced by selective harvest of larger fish over time. Finally, Alexander et al. (1979) reported that Michigan Department of Natural Resources spent about $250,000 on stream improvement during the 1970's, mostly in the Burton's Landing to Wakeley Bridge segment of the Main Au Sable.

Description of simulation example

The simulation example consisted of two parts. First, the population was simulated for a time period in the past, October 1972 to October

1978. Field data were available for this period from which model input values could be obtained, and no significant changes in growth or survival could be detected for the period. Regulations in effect for the 1973 through 1978 fishing seasons were: flies only, creel limit of 3 trout, 305-mm minimum size limit on brown trout, and harvest of trout was permitted from the end of April to the end of October. Starting in 1975, catch and release of trout (flies only) was permitted at anytime of the year, but no attempt was made to simulate the winter catch-and-release fishery. The simulation started with the fall 1972 population estimate as its initial population and used the survival and growth information for the 1972-78 period to predict the nature of the 1978 population. Under these circumstances, it was no surprise that the simulated population closely resembled the actual population. The exercise was not meant as a validation procedure, but as a demonstration of model performance.

In the second part of the example, the fishery was simulated for a time period in the future, October 1978 to October 1985. Regulations for the real fishery were changed with the 1979 season to: flies only, creel limit of 5 trout, harvest of trout between 203 and 305 mm and over 406 mm was permitted from the end of April to the end of October. Once again, catch-and-release fishing was permitted during winter, but was not simulated. The fall 1978 population estimate was used as the initial population, and survival and growth were assumed to remain unchanged from the earlier period. In addition to simulating the slot limits which were used in the real fishery, two other alternatives were tested, a 203-mm minimum size limit and a continuation of the 305-mm minimum size limit used from 1973-78.

Results from 1972-78 period

Input used to simulate the Au Sable brown trout fishery is listed in Appendix A.

Annual estimates of trout abundance from field data collected near October 1, 1972 to 1978, and a summary of fishery statistics produced by TROUT.DYNAMICS for the same period are given in Table 6. Even though the model maintained a constant annual fishing rate for the entire period (m = 0.30), a decline in harvest (C and Y in Table 6) of 35% from the 1972-73 fishing season to the 1977-78 season was predicted.

For the real fishery, Alexander et al. (1979) reported a decline of 72% in the harvest of brown and rainbow trout (305 mm and larger) from the early 1960's to 1976. Presumably, one or more of the events mentioned earlier caused this decline by changing growth, survival, and fishing rates between 1963 and 1972. For the simulated fishery, a continued decline in harvest from 1972 to 1978 can be traced directly to a decline in annual recruitment (Fig. 4).

Several other comparisons of simulated to real data are possible. First, the annual values of N which were calculated by TROUT.DYNAMICS can be compared to population estimates calculated from field data (Table 6). Second, Alexander et al. (1979) estimated the 1976 catch of brown trout from this section of the Au Sable was 10.9 per hectare. The simulated catch for the same time period was 12.3 trout per hectare. Finally, the length frequency of the October 1978 population which was calculated through 6 years of simulation can be compared to the length frequency from the fall 1978 population estimate (Fig. 5).

Since TROUT.DYNAMICS described seasonal variations in mortality and recruitment, it was possible to estimate the size of the harvestable stock throughout a typical fishing season (Fig. 6). Numbers of 305-mm and larger brown trout in the Burton-to-Wakeley section were lowest in the early part of the 1978 season and highest in mid-October. Apparently this trend is not unusual for brown trout populations. Data from Alexander (1974) and Gowing (1975) who studied North Branch of the Au Sable River and Gamble Creek respectively, showed that numbers of brown trout 305 mm+ were 60-65% higher in fall population estimates than in spring estimates.

Possibly the most useful feature of TROUT.DYNAMICS for evaluating regulations was its ability to estimate length frequencies of populations and catches (Table 7). Such information could be useful for defining regulations that maximize harvest of larger trout, maximize catch (but not necessarily harvest) of larger trout, compromise between harvest and catch and release of trout, or optimize the fishery for other pertinent management objectives.

Results from 1978-85 period

Same growth, mortality, and reproductive rates were used to simulate the 1978-85 fishery as were used for the earlier period (Appendix A), except that the fall 1978 population estimate was used as the initial population.

Continuation of 305-mm minimum limit.--Harvested catch appeared to be oscillating around 15 trout per hectare under the 305-mm regulation (Table 8). Assuming this figure is the equilibrium catch, then the simulated catch for 1984-85 (14.8 trout per hectare) provides a reasonable basis for comparing results of this regulation to the others. Table 9 shows length frequencies for this year.

Test of 203-mm minimum limit.--Substantial increases in harvested catch and yield (C and Y) and decreases in catch and release of trout (J and YJ) were predicted for the 203-mm size limit (Tables 6 and 10). This increased harvest was from trout in the 203- to 305-mm size category (Tables 7 and 11) which were formerly protected under the 305-mm limit.

The major disadvantage of the 203-mm size limit was the decreased harvest of trophy-size trout (i.e., 406 mm and larger). About 50% fewer trophy-size trout were caught in the 203-mm simulation as in the 305-mm simulation (Tables 9 and 11).

Test of slot size limits.--Equilibrium catch (harvested) was about 155 trout per hectare under slot limits, and equilibrium yield (harvested) was about 21 kg per hectare (Table 12). This was much greater than the harvest obtained under the 305-mm minimum limit, where the corresponding catch and yield were about 15 trout and 5.5 kg per hectare (Table 8). However, it was not as high as the 165 trout and 24 kg per hectare obtained under the 203-mm size limit (Table 10).

The sizable harvest obtained under the slot limit was accomplished without sacrificing much in the harvest of trophy-size trout. Catch of trout 406 mm and larger was only slightly less for the slot limits than for the 305-mm minimum limit (Tables 9 and 13).

Discussion

The mathematical techniques presented can be utilized to identify optimal regulations for many objectives relating to recreational fisheries management, such as maximizing catch of trophy-size trout. Or they can be used to find the best compromise between competing interests, such as maximizing total harvest versus maximizing catch of trophy fish. Effects of imposing almost any length limit, or combination thereof, can be analyzed with these techniques. Fishing mortality (m) and hooking mortality (mh) can be adjusted to simulate values typical for different gear types (e.g., artificial flies or live bait). Also, consequences of fluctuations in seasonal periodicity of growth and fishing mortality can be assessed, including shifts in fishing season length or time frame.

The main disadvantages of TROUT.DYNAMICS are its specialization for trout stream fisheries and its detailed data requirements. However, equations presented are of a general nature and could be used for other fisheries in the same manner as a typical dynamic pool model (i.e., on a yield per recruit basis).

The model was developed around a framework of biological statistics (Ricker 1975) which has received wide acceptance and use in fisheries science for many years. Thus, even though the model requires a detailed data set as input, it allows biologists to use and build upon data already in their files.

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Table 1.--Catch per hour for test fishermen during summer 1959 compared to estimated numbers of trout in fall 1959 population in the North Branch of the Au Sable River, Michigan. Fly water (special regulations) was from Otsego-Crawford county line to Eaman's Landing. Bait water (normal regulations) was from Dam 2 to Otsego-Crawford county line.

			Test fishing with			
			Artificial flies		Worms	
Size range (mm)	Population size (No/km)	Percentage of total population	Catch per hour	Percent of total catch per hour	Catch per hour	Percent of total catch per hour
			Fly Water			
0-177	6,826	78	3.58	77	2.11	47
178-228	1,566	18	0.83	18	1.94	43
229 +	353	4	0.22	5	0.47	10
Total	8,745	100	4.63	100	4.52	100
			Bait Water			
0-177	5,006	92	1.97	79	1.33	68
178-228	378	7	0.47	19	0.56	28
229 +	66	1	0.06	2	0.08	4
Total	5,450	100	2.50	100	1.97	100

Table 2.--Estimated survival in first 2 years of life for brook trout in Hunt Creek, Michigan, from 1949 to 1970.

Year	Egg production per ha	First year survival rate	Number age 0 per ha	Second year survival rate	Number age I per ha
1949	75,200		2,826		---
		0.033		0.450	
1950	75,800		2,491		1,272
		0.036		0.470	
1951	70,100		2,709		1,170
		0.045		0.411	
1952	64,500		3,181		1,114
		0.053		0.325	
1953	50,600		3,404		1,034
		0.079		0.378	
1954	65,700		3,997		1,286
		0.041		0.368	
1955	92,300		2,676		1,469
		0.034		0.381	
1956	84,700		3,127		1,019
		0.050		0.363	
1957	73,900		4,236		1,134
		0.044		0.396	
1958	95,400		3,221		1,676
		0.027		0.470	
1959	134,000		2,552		1,513
		0.024		0.549	
1960	104,900		3,196		1,401
		0.017		0.399	
1961	91,000		1,775		1,275
		0.035		0.566	
1962	89,100		3,193		1,004
		0.032		0.448	
1963	93,600		2,842		1,431
		0.027		0.418	
1964	74,700		2,491		1,188
		0.035		0.463	
1965	73,400		2,593		1,152
		0.039		0.465	
1966[a]	100,300		2,833		1,206
		0.034		0.313	
1967[a]	108,800		3,431		886
		0.035		0.325	
1968[a]	109,300		3,825		1,116
		0.043		0.354	
1969[a]	157,300		4,648		1,353
		0.020		0.263	
1970[a]	124,500		3,190		1,224
		0.030		0.380	
1971	---		3,760		1,212

[a] Scale samples from 1960-65 period were used to break population estimate into age groups.

Table 3.--Estimated survival in first 2 years of life for brook trout in upper section of the North Branch of the Au Sable River, Michigan, from 1959 to 1966.

Year	Egg production per ha	First year survival rate	Number age 0 per ha	Second year survival rate	Number age I per ha
1960	16,790		955		104
		0.086		0.152	
1961	24,166		1,452		145
		0.044		0.108	
1962	26,927		1,066		157
		0.023		0.211	
1963	31,505		606		225
		0.018		0.348	
1964	36,175		571		211
		0.022		0.378	
1965	40,604		779		216
		0.016		0.336	
1966	40,975		630		262
		0.006		0.476	
1967	---		252		300

Table 4.--Estimated survival in first 2 years of life for brown trout in upper section of the North Branch of the Au Sable River, Michigan, from 1959 to 1966

Year	Egg production per ha	First year survival rate	Number age 0 per ha	Second year survival rate	Number age I per ha
1960	23,832		292		49
		0.015		0.212	
1961	12,546		352		62
		0.028		0.324	
1962	26,742		351		114
		0.004		0.231	
1963	20,070		106		81
		---		0.481	
1964	43,662		28[a]		51
		0.005		---	
1965	35,452		77		48
		0.006		0.870	
1966	15,141		200		67
		0.005		0.465	
1967	---		74		93

[a] This appeared to be a low estimate and therefore was omitted from the regression analysis.

Table 5.--Estimated survival in first 2 years of life for brown trout in Gamble Creek, Michigan, from 1966 to 1972.

Year	Egg production per ha	First year survival rate	Number age 0 per ha	Second year survival rate	Number age I per ha
1966	97,734		956		335
		0.006		0.445	
1967	97,528		620		425
		0.009		0.869	
1968	87,531		844		539
		0.013		0.977[a]	
1969	97,346		1,127		825
		0.008		0.496	
1970	66,847		810		559
		0.015		0.642	
1971	106,430		979		520
		0.010		0.368	
1972	58,296		1,075		360

[a] This value was judged to be too high to be realistic and was therefore omitted from the regression analysis.

Table 6.--Annual population estimates (number per hectare) of brown trout from field data collected near October 1, and annual values of important statistics calculated by TROUT.DYNAMICS for 1972-78.

N = number per hectare in population on October 1
C = annual number per hectare of legal-size trout harvested
Y = annual yield in kilograms per hectare of harvest
J = annual number per hectare of illegal-size trout caught and released
YJ = annual yield in kilograms per hectare of trout caught and released
H = annual number per hectare of deaths due to hooking mortality
D = annual number per hectare of natural deaths
P = annual biomass production in kilograms per hectare

Period[a]	Population estimate from field	N	C	Y	J	YJ	H	D	P
1972-73	2162.4	2162.4	20.3	7.3	341.4	34.2	17.0	1086.5	157.0
1973-74	1907.4	1566.0	17.8	6.3	283.1	30.1	14.1	705.3	146.5
1974-75	1936.7	1651.3	16.1	5.6	248.5	25.0	12.4	836.3	141.0
1975-76	2157.6	1838.1	13.1	4.7	262.2	23.6	13.0	959.5	139.5
1976-77	1888.8	2192.4	11.3	4.0	308.7	27.7	15.4	1167.6	146.7
1977-78	1597.5	2436.9	13.0	4.5	345.8	31.7	17.2	1312.5	160.6
1978-	2397.1	2385.6							

[a] From October 1 of first year listed to October 1 of second year listed.

Table 7.--Length frequency of population predicted for October 1, 1977, and of catches predicted for the month of October 1977 plus months of May through September 1978. A minimum size limit of 305 mm was placed on harvest of trout with a conditional fishing rate of 0.30.

Length range (mm)	Population (no./ha)	Harvested catch (no./ha)	Catch and release (no./ha)
25-50	13.1	0.0	0.0
51-75	422.4	0.0	0.0
76-101	688.6	0.0	0.0
102-126	288.5	0.0	0.0
127-151	67.7	0.0	29.0
152-177	182.1	0.0	73.4
178-202	252.4	0.0	70.6
203-228	137.2	0.0	60.9
229-253	170.4	0.0	57.8
254-278	114.6	0.0	35.8
279-304	56.3	0.0	18.3
305-329	26.8	8.1	0.0
330-355	11.4	3.4	0.0
356-380	3.1	0.9	0.0
381-405	0.7	0.3	0.0
406+	1.6	0.3	0.0
Totals	2436.9	13.0	345.8

Table 8.--Annual values of important statistics calculated by TROUT. DYNAMICS for 1978 to 1985 under 305-mm minimum size limit.

N = number per hectare in population on October 1
C = annual number per hectare of legal-size trout harvested
Y = annual yield in kilograms per hectare of harvest
J = annual number per hectare of illegal-size trout caught and released
YJ = annual yield in kilograms per hectare of trout caught and released
H = annual number per hectare of deaths due to hooking mortality
D = annual number per hectare of natural deaths
P = annual biomass production in kilograms per hectare

Period[a]	N	C	Y	J	YJ	H	D	P
1978-79	2397.1	12.9	4.6	299.6	26.0	14.9	1378.1	149.7
1979-80	2342.1	12.2	4.3	344.9	31.1	17.2	1224.7	157.1
1980-81	2463.6	14.7	5.0	364.0	34.9	18.1	1298.6	167.3
1981-82	2265.4	17.3	5.9	349.3	34.2	17.4	1160.5	163.4
1982-83	1912.2	17.2	5.9	316.9	32.1	15.8	920.4	155.6
1983-84	1846.3	16.6	5.8	288.3	28.8	14.3	921.9	149.8
1984-85	1861.9	14.8	5.2	281.8	26.9	14.0	943.0	147.2

[a] From October 1 of first year listed to October 1 of second year listed.

Table 9.--Length frequency of population predicted for October 1, 1984, and of catches predicted for the month of October 1984 plus months of May through September 1985. A minimum size limit of 305 mm was applied under a fishing rate of 0.30.

Length range (mm)	Population (no./ha)	Harvested catch (no./ha)	Catch and release (no./ha)
25-50	8.8	0.0	0.0
51-75	284.4	0.0	0.0
76-101	463.6	0.0	0.0
102-126	194.4	0.0	0.0
127-151	49.4	0.0	22.1
152-177	143.3	0.0	57.0
178-202	200.3	0.0	55.6
203-228	116.4	0.0	48.8
229-253	154.2	0.0	48.2
254-278	121.2	0.0	32.3
279-304	67.9	0.0	17.8
305-329	33.8	8.5	0.0
330-355	16.5	4.0	0.0
356-380	4.9	1.3	0.0
381-405	0.9	0.5	0.0
406+	1.9	0.5	0.0
Totals	1861.9	14.8	281.8

Table 10.--Annual values of important statistics calculated by TROUT. DYNAMICS for 1978 to 1985 under 203-mm minimum size limit.

N = number per hectare in population on October 1
C = annual number per hectare of legal-size trout harvested
Y = annual yield in kilograms per hectare of harvest
J = annual number per hectare of illegal-size trout caught and released
YJ = annual yield in kilograms per hectare of trout caught and released
H = annual number per hectare of deaths due to hooking mortality
D = annual number per hectare of natural deaths
P = annual biomass production in kilograms per hectare

Period[a]	N	C	Y	J	YJ	H	D	P
1978-79	2397.1	133.4	20.5	162.6	7.3	8.1	1358.8	144.7
1979-80	2281.1	148.5	20.9	173.5	8.1	8.6	1177.3	139.7
1980-81	2459.2	163.5	23.4	175.3	8.1	8.7	1297.9	147.7
1981-82	2474.9	166.0	23.9	177.0	8.2	8.8	1308.1	152.1
1982-83	2421.2	167.9	24.3	173.9	8.2	8.6	1260.3	151.9
1983-84	2411.2	166.2	24.1	172.4	8.0	8.5	1259.9	151.7
1984-85	2392.5	164.1	23.9	171.8	8.0	8.5	1248.1	150.8

[a] From October 1 of first year listed to October 1 of second year listed.

Table 11.--Length frequency of population predicted for October 1, 1984, and of catches predicted for the month of October 1984 plus months of May through September 1985. A minimum size limit of 203 mm was applied under a fishing rate of 0.30.

Length range (mm)	Population (no./ha)	Harvested catch (no./ha)	Catch and release (no./ha)
25-50	12.9	0.0	0.0
51-75	415.8	0.0	0.0
76-101	677.9	0.0	0.0
102-126	284.1	0.0	0.0
127-151	68.2	0.0	28.7
152-177	187.8	0.0	73.2
178-202	259.3	0.0	69.9
203-228	135.5	57.8	0.0
229-253	163.2	51.7	0.0
254-278	103.0	29.8	0.0
279-304	47.4	14.4	0.0
305-329	22.8	6.4	0.0
330-355	10.2	2.7	0.0
356-380	2.9	0.8	0.0
381-405	0.5	0.3	0.0
406+	1.0	0.2	0.0
Totals	2392.5	164.1	171.8

Table 12.--Annual values of important statistics calculated by TROUT. DYNAMICS for 1978 to 1985 under slot size limit (harvest from 203-305 mm and over 406 mm).

N = number per hectare in population on October 1
C = annual number per hectare of legal-size trout harvested
Y = annual yield in kilograms per hectare of harvest
J = annual number per hectare of illegal-size trout caught and released
YJ = annual yield in kilograms per hectare of trout caught and released
H = annual number per hectare of deaths due to hooking mortality
D = annual number per hectare of natural deaths
P = annual biomass production in kilograms per hectare

Period[a]	N	C	Y	J	YJ	H	D	P
1978-79	2397.1	122.8	17.1	174.4	11.4	8.7	1363.3	145.5
1979-80	2276.7	141.0	18.6	182.1	11.3	9.0	1176.9	141.8
1980-81	2450.7	155.2	21.0	183.9	11.3	9.1	1294.8	149.3
1981-82	2459.9	156.2	21.0	186.7	11.8	9.3	1301.3	153.4
1982-83	2396.3	157.7	21.3	183.2	11.8	9.1	1246.3	153.0
1983-84	2382.2	155.5	21.1	181.6	11.7	9.0	1244.1	152.6
1984-85	2360.6	153.2	20.8	180.8	11.7	9.0	1230.5	151.6

[a] From October 1 of first year listed to October 1 of second year listed.

Table 13.--Length frequency of population predicted for October 1, 1984, and of catches predicted for the month of October 1984 plus months of May through September 1985. Harvest of trout between 203 and 305 mm and over 406 mm was permitted under a conditional fishing rate of 0.30.

Length range (mm)	Population (no./ha)	Harvested catch (no./ha)	Catch and release (no./ha)
25-50	12.7	0.0	0.0
51-75	407.3	0.0	0.0
76-101	664.0	0.0	0.0
102-126	278.3	0.0	0.0
127-151	67.2	0.0	28.3
152-177	185.8	0.0	72.3
178-202	256.6	0.0	69.2
203-228	134.2	57.3	0.0
229-253	161.9	51.3	0.0
254-278	103.4	29.7	0.0
279-304	48.2	14.5	0.0
305-329	23.7	0.0	6.6
330-355	11.5	0.0	3.0
356-380	3.4	0.0	1.0
381-405	0.7	0.0	0.4
406+	1.7	0.4	0.0
Totals	2360.6	153.2	180.8

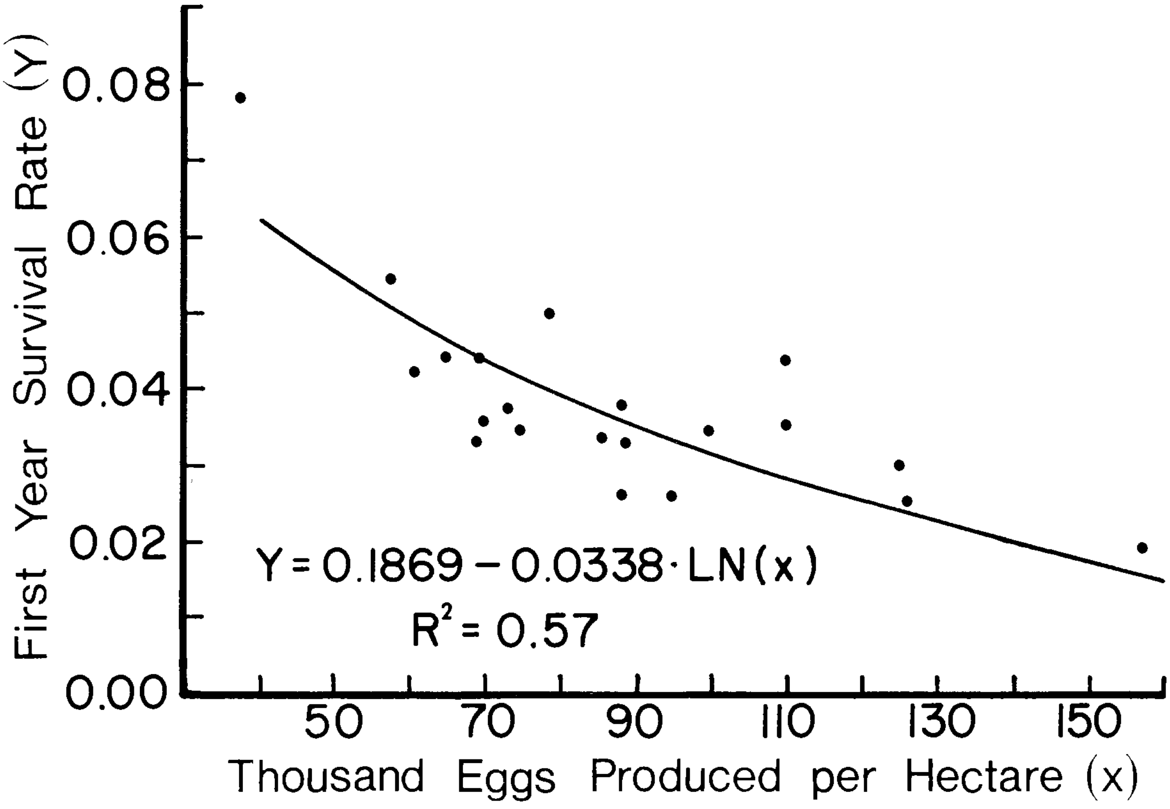

Figure 1.--First year survival rate versus estimated egg production per hectare for brook trout in Hunt Creek, Michigan, 1949 to 1970.

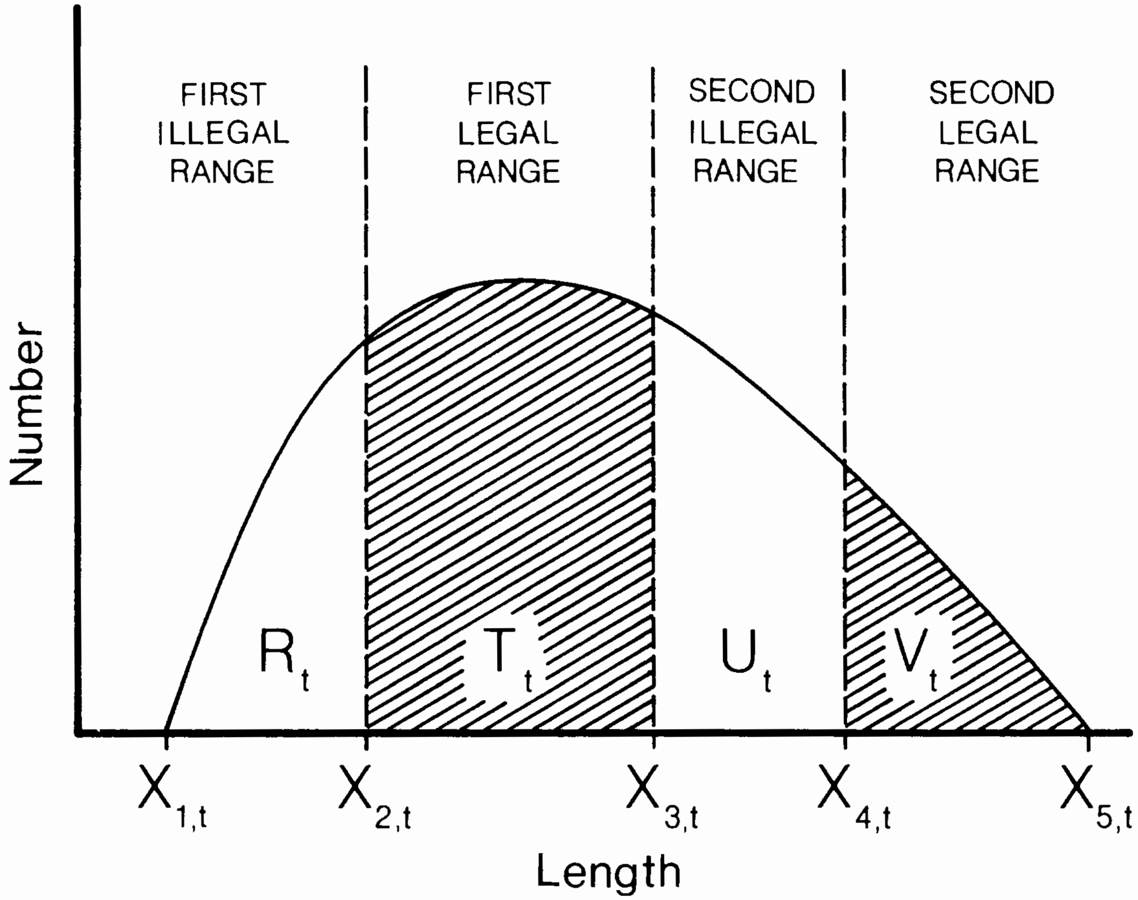

Figure 2.--Hypothetical length-frequency distribution of a trout cohort being fished under slot size limit regulations. Trout in cross-hatched areas T and V are legal for harvest, while those in areas R and U are illegal.

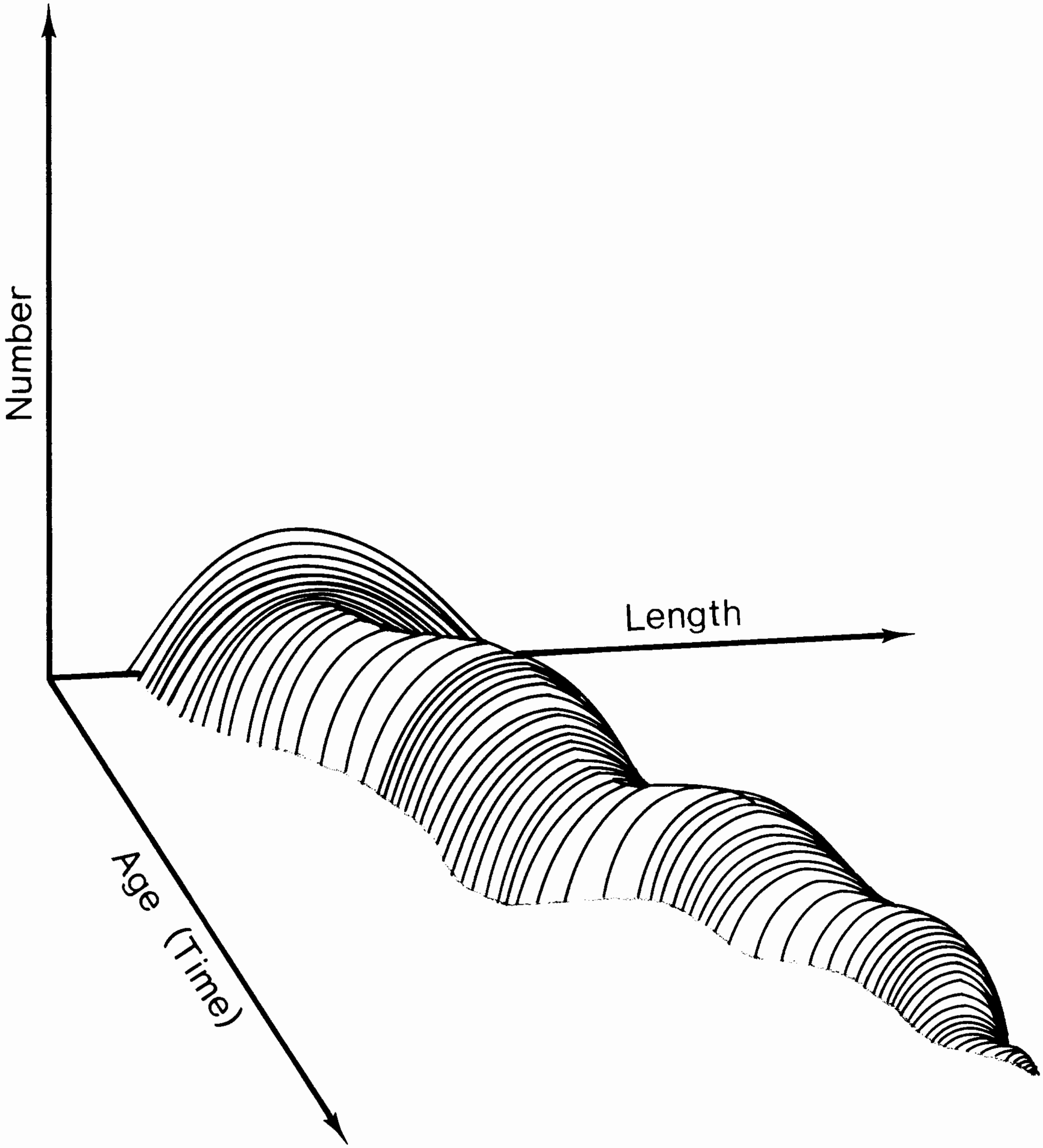

Figure 3.--Visual model of changes in numbers and sizes in a trout cohort over time.

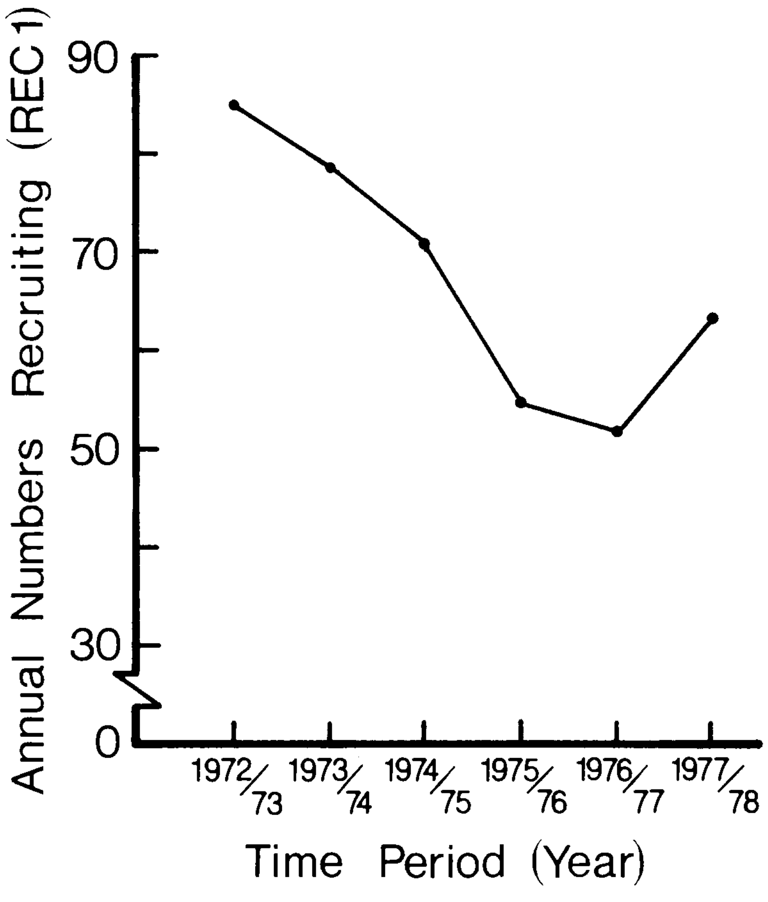

Figure 4.--Trend in recruitment predicted by TROUT.DYNAMICS for Au Sable brown trout fishery with a 305-mm minimum size limit.

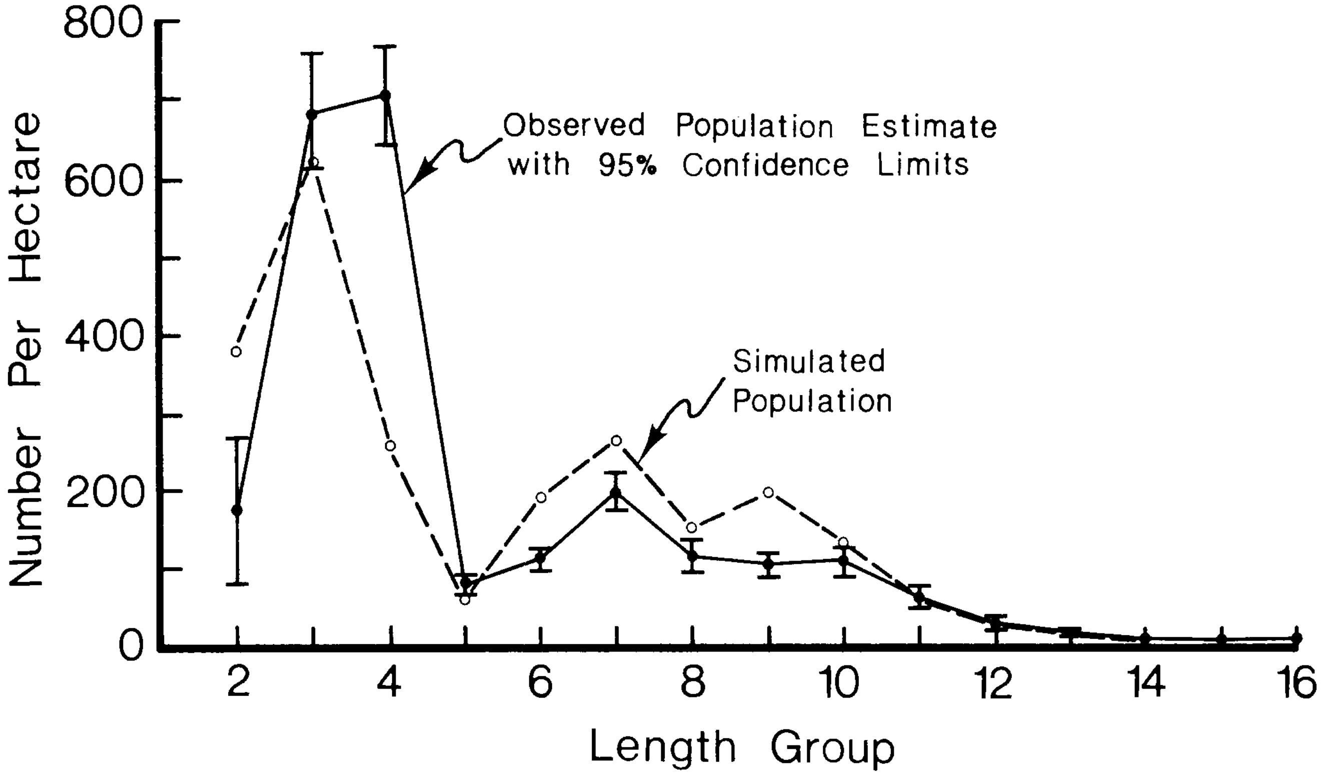

Figure 5.--Length frequency of the fall 1978 brown trout population as determined from data collected in field versus length frequency of simulated population for 1978.

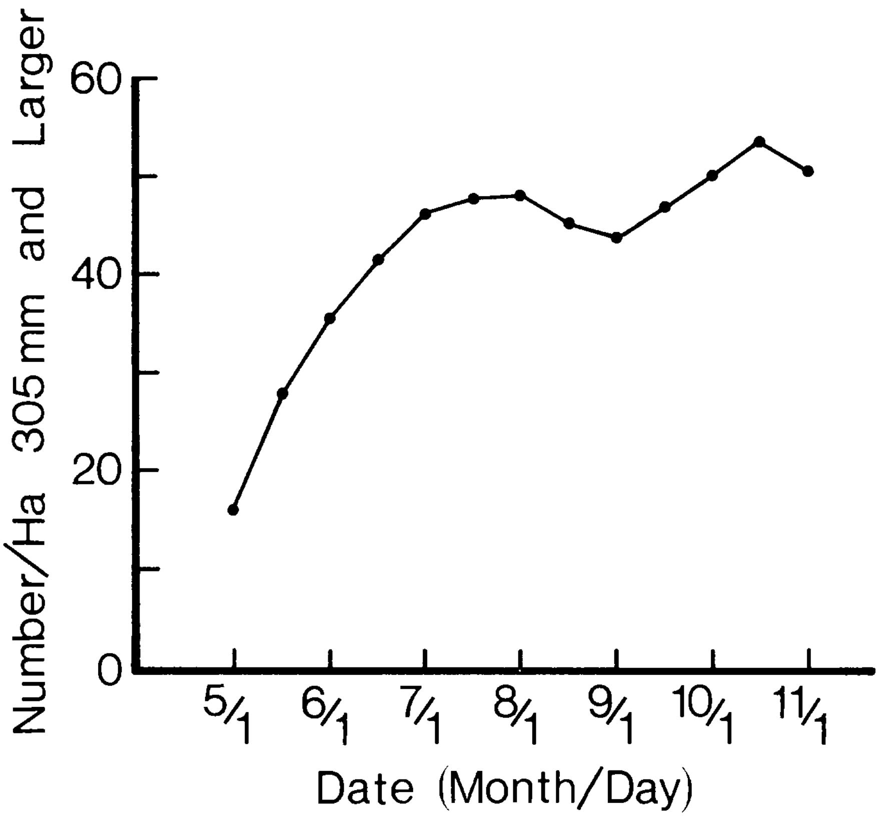

Figure 6.--Model calculation of the size of harvestable brown trout stock through the 1978 fishing season in the Burton-to-Wakeley section of the Main Au Sable River. A 305-mm minimum size limit was in effect.

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Typed by M. S. McClure

APPENDIX A.--List of input values used to simulate Au Sable River brown trout fishery from 1972-78.

1. Conditional fishing mortality rate (annual): $m = 0.30$

2. Probability of death due to hook and release set to approximate flies-only rules: $h = 0.05$

3. Conditional natural mortality rates (annual) for first 2 years of life as a function of density:

$$\text{Egg to age } 0 = n_1 = 1 - [0.14861 - 0.03016\, \ell n(\frac{\text{eggs/ha}}{1000})]$$

$$\text{Age } 0 \text{ to } 1 = n_2 = 1 - [1.5942 - 0.16966\, \ell n(\text{number age } 0/\text{ha})]$$

4. Conditional natural mortality rates (annual), mean lengths (mm), and initial number present per hectare in each age group

Age	n	Mean length	Number present
0	-	91	1011.7
1	0.23	175	480.4
2	0.39	236	391.7
3	0.91	285	246.4
4	0.80	243	27.5
5	0.80	401	4.7
6	0.90	446	0.0
7	0.95	490	0.0
8	0.95	532	0.0
9	1.00	570	0.0

5. Description of length frequencies for each age group on October 1

Age	Length (mm)		
	Shortest	Modal	Longest
0	43	84	173
1	107	183	239
2	158	239	300
3	239	274	419
4	262	345	399
5	350	415	450
6	420	446	475
7	440	490	540
8	490	532	580

6. Description of reproductive potential (from North Branch of the Au Sable brown trout population data of Alexander 1974)

Length range (mm)	Percent females	Percent sexually mature	Mean egg number
<203	50	0	0
203-228	50	20	328
229-253	50	43	482
254-278	50	63	637
279-304	50	80	791
305-329	50	91	945
330-355	50	100	1100
356-380	50	100	1254
381-405	50	100	1409
406-431	50	100	1568
432-456	50	100	1810
457-482	50	100	2073
483-507	50	100	2357

7. Minimum size of trout vulnerable to fishing gear = 140 mm