

The Effects of Fishing Regulations on Annual Fluctuations in Abundance and Harvest

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Abstract

I simulated fluctuating year-class strength in a brown trout (Salmo trutta) fishery to estimate how the annual variability in population size and harvest was affected by exploitation under different minimum size limits and fishing mortality rates. My model included realistic details common to many fish populations in temperate regions; discrete annual reproduction and age-specific natural mortality, maturity, and fecundity. I hypothesized the primary mechanism regulating population size was density-dependent mortality in early life, but also that early mortality had a density-independent component which varied due to random environmental factors. I proposed a new method of representing this hypothesis quantitatively and of interpreting it ecologically. I conducted two series of stochastic simulations in which random variation was introduced at different stages of year-class formation. In the first, a range of instantaneous fishing mortality rates from 0.0 to 2.0 was simulated for 60 years each while the minimum size limit was held constant at 229 mm. In the second, a range of minimum size limits from 120 mm to 305 mm was simulated for 60 years each while the instantaneous fishing mortality rate was held constant at 0.7. Coefficients of variation ($100 s/\bar{x}$) for mean population sizes and harvests were used to compare relative variability between simulations. I found that the number of fish in the simulated populations had minimum variability when exploited near maximum sustainable yield (MSY) in weight, fishing rates of 0.6 to 1.6 at the 229-mm size limit and size limits of 150 mm to 250 mm at the 0.7 fishing rate. Simulated populations were highly variable when lightly exploited because the compensatory-density-dependent response was strong enough to overshoot the population's equilibrium level after a random disturbance. As exploitation increased, it reduced the strength of the density-dependent

response. Near MSY, the strength of density dependence was about equal to the strength of random disturbances, and this minimized variation in population size. Higher exploitation reduced the strength of density dependence to where it could not fully compensate for random disturbances, so variability increased. Variability of harvests did not match variability of populations because they had different age structures, a normal consequence of minimum size limit regulations or gear selectivity. Changing the fishing rate had little effect on variability of harvest, but changing the size limit from 120 mm to 305 mm increased the coefficient of variation of harvest from 13% to 44% when the standard deviations of random year-class fluctuations were 50% of their means. I concluded that for fisheries with fluctuating year-class strength, variability in annual catch is minimized by maintaining the lowest practical size limit and managing the fishery by controlling fishing effort.

Introduction

Fish populations fluctuate in size due to factors which appear to occur at random, such as variable food production or weather conditions. Fisheries managers often consider such fluctuations as unavoidable and uncontrollable facts of nature, but the strength of a population to resist these fluctuations depends on its ability to compensate for unexpected losses or gains by changing growth, mortality, or reproductive rates, all of which are affected by exploitation. Hence, because exploitation is under the control of the manager, he can also control fluctuations in the fishery, at least to some extent. For fishermen, fluctuating catches resulting from fluctuating populations can be both a nuisance and an economic hardship. Thus, it seems important for managers to consider the way harvest level and management alternatives affect the variability of fisheries.

In general, fisheries can be managed by either adjusting fishing mortality (effort) or minimum size limit (age of entry). The purpose of my study was to estimate how the variability of fish populations and harvests might be related to the choice of managing by one or a combination of these alternatives. Previous studies on population stability have dealt with the effects of changing fishing mortality (Doubleday 1976; Beddington and May 1977; Sissenwine 1977; Shepherd and Horwood 1978; Horwood and Shepherd 1981), but none have addressed the effects of changing size limits. I used an age-structured model of a brown trout (Salmo trutta) fishery for my analysis which was realistic to the extent that it contained randomly fluctuating year-class strength with density-dependent and density-independent components, discrete annual reproduction, and age-specific natural mortality, maturity, and fecundity.

Throughout this report I will be using the terms variability and stability in reference to populations and harvests. As they are commonly used these two words are usually intended to have opposite meanings; something stable is not variable. However, this inverse relationship may be a poor one when dealing with animal populations (Horwood and Shepherd 1981). I will show later that a stable population can be highly variable if its compensatory mechanisms are stronger than needed to adjust for the observed level of uncertainty in the environment. Thus, it will be important for the reader to distinguish between the two terms and to be aware of what I mean when I use them in the text. I will use stability in biological contexts to mean the strength to resist change, to stand firm and endure, or the inherent property of returning to an equilibrium level when disturbed instead of increasing toward infinity or decreasing to extinction. In contrast, I will use variability in statistical contexts to mean a measure of the observed deviations from a mean value.

Description of Model

Shepherd and Horwood (1978) cautioned against making generalizations concerning the effect of exploitation on population stability and variability. They showed the effect was dependent on the nature of the mechanisms regulating population size and the manner in which the population was perturbed. They concluded that models intended for the analysis of stability and variability were more demanding of realism than those typically used for calculating equilibrium yield, particularly in the nature and form of the density-dependent responses operating.

There are many ways in which random environmental changes affect fish populations, but fluctuating year-class strength is probably the most common and widely recognized (Cushing 1977, Koonce et al. 1977). Fluctuations have been

attributed to density-dependent processes inherent to the population (Larkin and McDonald 1968; Larkin 1971; Chevalier 1973; Forney 1976) and to random environmental factors (Lawler 1965; Busch et al. 1975; Shuter et al. 1980). In most cases, year-class strength is probably influenced to some extent by both density and environmental factors, with the former being the compensatory force which moves the population toward equilibrium and the latter being the random force which disturbs the population from equilibrium. A model which incorporates both density and environmental effects on year class formation would realistically represent the population fluctuations existing in a large number of fisheries.

The population model was first described in an earlier paper (Clark et al. 1980). Its original purpose was to study the effects of fishing regulations on trout-stream fisheries. For this analysis, I simplified the model by changing the way in which the growth of individual fish was expressed and by removing the detailed description of the length-frequency of the population. Such detail was useful for analyzing fishing regulations, but it was not needed for this analysis. I also revised the manner of expressing the density-dependent mortality of young fish. This revision did not change the qualitative behavior of the model, but it provided parameters which were more meaningful in a biological sense, making the dynamics of the model easier to interpret. A full description of the revised model will be given later.

Data used to develop the original model, and which still applies to the revised model, came from three trout streams in the north central 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, and

the North Branch of the Au Sable River supported both brook and brown trout. Data from these streams were collected with direct-current electrofishing gear and included (1) semiannual (mid-April and mid-September to mid-October) estimates of trout density within size and age categories; (2) estimates of catch by age; (3) analyses of growth, condition, fecundity, and sexual maturity. Also, the data were collected under a wide variety of conditions with respect to exploitation. Brook trout populations from Hunt Creek and brown trout populations from Gamble Creek have been monitored through years in which fishing was permitted (from 1945 to 1965 on Hunt Creek, from 1961 to 1965 on Gamble Creek), and through years in which fishing was prohibited (from 1966 to 1979 on Hunt Creek and from 1966 to 1973 on Gamble Creek). The fishery on the North Branch of the Au Sable River has been monitored from 1960 to 1967 and from 1972 to 1983. Detailed descriptions of these fisheries and the data collection procedures were given by McFadden et al. (1967), Shetter (1969), Gowing (1975), Alexander and Ryckman (1976), Alexander (1977a, 1977b), and Alexander et al. (1979).

Backiel and Le Cren (1978) proposed a simple but useful approach for studying and describing the dynamics of fish populations. They suggested dividing the life span of a fish into two phases: (1) early life when year-class strength is formed and factors controlling population growth have their greatest effect through mortality; and (2) adult life when mortality changes are of minor importance, excepting exploitation, but growth may vary with density. This was the basic approach I used to develop the population model, except that I could not find any significant expression of density-dependent growth in trout in Michigan streams (Clark et al. 1980). Thus, I assumed that (1) growth in early life (below 18 months of age) was constant but mortality was density-dependent, and (2) both growth and mortality were constant in adult life (over 18 months of

age). This means that the only mechanism regulating the size of the population in the model was the density-dependent mortality of young fish. Based on the field data available for trout in Michigan streams, a model with these assumptions appears to represent very closely what actually happens in the real populations (McFadden et al. 1967; Clark et al. 1980). I am not suggesting that the capacity for density-dependent growth or other regulatory mechanisms does not exist in the real populations, but only that the density-dependent mortality of the young is the primary regulatory mechanism. This mechanism appears to be so effective that it precludes the need for the other mechanisms to come into play under most circumstances.

The importance of density-dependent mortality of the young is not unique to trout stream fisheries but has been recognized as being one of the most important mechanisms regulating the size of fish populations in general (Ricker 1954; Cushing 1977; Backiel and Le Cren 1978). The actual cause of the density-dependent mortality may be quite different from one species to another (for example, it could be caused by territoriality, cannibalism, or food competition), but the effects on the population dynamics are similar. Therefore, while my analysis will use the brown trout population in the Au Sable River as a case study, the basic results will apply in general to any population with discrete annual reproduction which is regulated in size by the density-dependent mortality of the young.

My model was age-structured, retaining each individual cohort in a population matrix. Mortality was density-dependent for fish younger than 18 months but was treated in a manner similar to that of a standard dynamic pool model for older fish (Beverton and Holt 1957):

$$(1) \quad \begin{array}{ll} dN/dx = -MN & 1 \leq x < x_c \\ dN/dx = -(M + F)N & x_c \leq x \\ dC/dx = FN & x_c \leq x \end{array}$$

Where: M was the instantaneous natural mortality rate,
 F was the instantaneous fishing mortality rate,
 C was the catch in numbers,
 x was the age of the fish,
 x_c was the age of first harvest.

Average length was related to age by the von Bertalanffy growth function.

The model was executed in discrete time steps of 1 year in the manner of Clark and Huang (1983). This permitted the simulation of realistic details common to most fishes in temperate regions; discrete annual reproduction and age-specific natural mortality, maturity, and fecundity.

The most important feature of the model, as it related to the stability analysis, was the mechanism used for population regulation. My basic hypothesis was that competition for space (territoriality) in the first 2 years of life was the primary mechanism regulating population size. As mentioned earlier, I assumed this competition resulted in density-dependent mortality of juveniles and precluded further population adjustments, such as density-dependent growth, maturity, fecundity, or mortality of adults. This assumption agrees with results obtained in field and laboratory experiments on stream salmonids (Kalleberg 1958; Chapman 1962, 1966; Le Cren 1965; Mason and Chapman 1965; Allen 1969; McFadden 1969; McFadden et al. 1967; Slaney and Northcote 1974; Backiel and Le Cren 1978; Fausch 1982).

The mathematical relationships used to describe density-dependent mortality were:

$$\begin{aligned}
 & dN/dx = -(M_0 + \beta_0 N)N & 0 \leq x < 1 \\
 (2) \quad & dN/dx = -(M_1 + \beta_1 N)N & 1 \leq x < 2
 \end{aligned}$$

Where: $N(0)$ represented the number of eggs produced by the adult stock each fall (brown trout spawn in the fall),

$N(1)$ represented the number of age-0 fish present at spawning time (brown trout eggs hatch in spring, so these fish would be about 6 months old),

M_0 and M_1 were density-independent mortality coefficients for the first and second years of life, respectively, and

β_0 and β_1 were density-dependent mortality coefficients representing the depressing effects of intraspecific competition (territoriality for stream trout).

The general solution of equation (2) for 1 year's mortality is:

$$(3) \quad N(x + 1) = N(x) \exp[-M_x - \beta_x N(x)]$$

This equation has mathematical properties identical to Ricker's stock-recruitment equation (Ricker 1954):

$$(4) \quad R = A P \exp(-BP)$$

Where: R = recruits,

P = parent stock,

A = density-independent parameter, and

B = density-dependent parameter.

That is equation (3) can be written as:

$$-\log_e [N(x + 1)/N(x)] = M_x + \beta_x N(x),$$

and the equation (4) can be written as:

$$-\log_e \{R/P\} = \log_e (A) + BP.$$

Therefore, in a mathematical context, $N(x + 1)$ equals R , $N(x)$ equals P , M_x equals $\log_e(A)$, and β_x equals B . However, it should be recognized that these variables do not have equivalent meanings in the biological context.

The parameters M_x and β_x were estimated empirically from a series of annual abundance estimates by assuming the total instantaneous mortality rate (Z_x) for a year is:

$$(5) \quad Z_x = -\log_e [N(x + 1)/N(x)] = M_x + \beta_x N(x).$$

A simple linear regression in which the independent variable was $N(x)$ and the dependent variable was $-\log_e [N(x + 1)/N(x)]$ gave a slope equal to β_x and an intercept equal to M_x (Fig. 1).

After M_x and β_x are estimated, the model can be applied to calculate $N(x + 1)$ for a range of values of $N(x)$. This gives a curve with a dome which was interpreted biologically as the carrying capacity ($K_{x + 1}$) of the stream for age $x + 1$ fish (Fig. 2). Setting the derivative of equation (3) equal to zero gives an equation for the number of fish of age x corresponding to the maximum number surviving to age $x + 1$:

$$(6) \quad N(x) = 1/\beta_x$$

and substituting this expression for $N(x)$ back into equation (3) gives a simple equation for the carrying capacity of age $x + 1$ fish:

$$(7) \quad K_{x+1} = \exp(-M_x - 1) / \beta_x$$

Obviously, if a stream has a carrying capacity for one or more age groups of fish in a population, the overall population is limited in size also.

Simulation Analysis

Annual estimates of brown trout abundance and growth have been conducted by the Michigan Department of Natural Resources for many years in the Mainstream of the Au Sable River (Alexander et al. 1979). The nature of these data was the same as the data described earlier for other Michigan trout streams. These data for the period 1974 to 1979 were used to estimate model parameters for a case study (Table 1).

Qualitative Behavior of Model

Before proceeding with the analysis of variability, the qualitative behavior of the model was examined in two tests to determine if it was realistic. In the first test, trajectories of population growth were calculated, starting with 100 age-1 fish per hectare, for an unexploited and an exploited case (120 mm minimum size limit and $F = 0.70$). The results of this test showed that the population trajectories for my model were similar to those of a simple logistic model in the form of a discrete-difference equation (May et al. 1974), except for some unevenness in its approach to carrying capacity that was caused by the presence of age structure (Fig. 3). The trajectory for the unexploited population overshot the equilibrium level (or carrying capacity) of 1,000 fish per hectare (age 1 or

older) by the eighth year of simulation and then display damped oscillations. The equilibrium level of the exploited population was 420 fish per hectare (age 1 or older), and the population grew much slower than the unexploited one. Its approach to equilibrium was monotonically damped, and the population had not quite reached equilibrium after 30 years of simulation. The fact that the unexploited population overshoots its equilibrium level, and the exploited population does not, will be important later when the effects of exploitation on variability are examined.

In the second test, simulations were conducted to explore the relationship between exploitation and the characteristic return time which describes the typical time it takes the population to return to its equilibrium level after a small disturbance (May et al. 1974; May 1975; Beddington and May 1977). Return time is typically used as an index of stability. I disturbed the equilibrium populations at four different levels of exploitation by reducing the number of age-1 fish by 90% in the fourth year of a 30-year simulation. Exploitation was controlled in these simulations by adjusting the minimum size (or age) of harvest, while the fishing mortality rate (F) remained constant at 0.7. The results of this test were that the model again behaved as a logistic equation in the sense that its characteristic return time (T_R) was inversely related to the level of exploitation (Fig. 4). The unexploited population overshoot its equilibrium level of 1,000 fish, 4 years after the disturbance and then displayed damped oscillations. As size limit was reduced and more of the population was subjected to exploitation, the first response was a decrease in the amplitude of the overshooting oscillations followed by an increase in the characteristic response time. My conclusion from these tests was that the model as it was constructed was well behaved in a qualitative sense, because it performed within the bounds of

what was expected based on accepted population dynamics theory.

Variability Versus Exploitation

Methods

I conducted two series of simulations. In the first, exploitation was controlled by adjusting the fishing mortality rate while size limit was constant. A range of fishing mortality rates (F) from 0.0 to 2.0 was used while the minimum size limit was held at 229 mm ($x_c = 2.0$). In the second series, I controlled exploitation by adjusting the minimum size of harvest and kept fishing rate constant. Minimum size limits from 120 mm to 305 mm were used while the fishing mortality rate was maintained at 0.70. These two series of simulations did not cover all possible combinations of fishing rate and size limits, but they did provide a cross section of the practical range of regulations that might be applied to a population with the growth rate and size distribution of this brown trout fishery.

Within each of these two series, I further divided the simulations into two smaller groups, one for each of two different methods of introducing random variation. In other words, the full range of fishing rates was simulated twice in series 1 and the full range of size limits was simulated twice in series 2. In the first group of simulations in each series, I introduced year-class fluctuations by adding a normally distributed random variable (r), with a mean of zero and a standard deviation of 0.5, to the number of eggs produced each year. This type of random variation might arise in nature if egg hatching rate or larval survival rate varied with weather conditions or food availability at time of hatching. In the second group of simulations in each series, I introduced year-class fluctuations by adding the random variable (r) to the number of fish surviving to age 1. This type of random variation might arise in nature for

the same reasons as the first method, but would also simulate variability in the effectiveness of density-dependent mortality in correcting any initial variation in egg or fry production. Thus, the second method causes a greater degree of variability in year classes entering the fishery than the first method, and this distinction will prove to have important effects on the results. Both of these methods of introducing variation assume environmental fluctuations are normally distributed random variables which have no trend over time.

Deterministic simulations were conducted to calculate the equilibrium population sizes for each level of exploitation. These equilibrium populations were then used as the initial populations for 60-year stochastic simulations in which year-class strength fluctuated at random as described above.

The random variables (r) were generated by a system subroutine, GRAND, supplied by the University of Michigan Computing Center. This subroutine required an initial random number seed, and it used the power-residue method and the central limit theorem to compute normally distributed random numbers with a given mean and standard deviation (University of Michigan Computing Center 1976). The same random number seed was used for all simulations, and each individual value generated for r was used only once in any given simulation. Means and standard deviations of the annual population sizes and catches were calculated for all stochastic simulations. Coefficients of variation ($100 s/\bar{x}$) were used to compare the relative variability between simulations.

Results

In general, simulation results showed that annual population size was least variable (had smallest coefficient of variation) for intermediate levels of exploitation, fishing rates of 0.6 to 1.6 at the 229 mm size limit and

size limits of 150 mm to 250 mm at the 0.7 fishing rate (Fig. 5). These rates of harvest did not produce maximum catches in number, but did produce near maximum yields in weight as determined by a previous study (Clark 1981).

Variability of annual harvest was nearly constant over the entire range of fishing mortality rates in the first series of simulations, although catches were less variable when variation was introduced at the egg stage than the age-1 stage (Fig. 6). In the second series of simulations, the annual catch was least variable at an intermediate size limit (about 200 mm) when variability was introduced at the egg stage, but was least variable at the lowest size limit (120 mm) when variability was introduced at age 1. Variability of annual harvests increased considerably as size limit increased in this latter case, with the coefficient of variation increasing from 13% at a 120-mm size limit to 44% at a 305-mm size limit.

The variability of the catch did not reflect the variability of the population (Figs. 5 and 6). This is a potentially important consequence of having a different number of age groups in the catch than in the population. The details of how this can occur are discussed later, but it means that caution should be used when evaluating the variability or stability of a population using catch data. The catch data will accurately reflect the variability of the population only if all age groups are presented in the catch in proportion to their abundance in the population. Unfortunately, this condition is rarely ever met in a real fishery because of gear selectivity or minimum size limit regulations.

Examining Causes of Variability

Two major factors were responsible for the trends in variability I observed: the nature of the density-dependent mortality relationship and the age structure of the

population and catch. The effects of these two factors can be explained by considering how fluctuating year-class strength resembles a single-factor analysis of variance (ANOVA) experiment where the number of treatment levels equals the number of age groups present. In this context, I will discuss variability in catch, but variability in the population could be evaluated in the same way.

Considering each age group as a separate treatment level and the number caught per age as individual observations, one can compute treatment means (mean catch by age group) and variances using the same formulas as in a single-factor ANOVA experiment. However, the mean total catch is not analogous to the grand mean of ANOVA, because total annual catches are equal to the sum of the observed catches for each treatment level (catches by age). For the same reason, the sum of squares within treatments and between treatments do not add to equal the sum of squares for the total annual catch.

The standard statistical formula for calculating the variances (s^2) associated with the mean total catch is:

$$(8) \quad s^2 = \frac{\sum_{i=1}^n (C_i - \bar{C})^2}{(n - 1)}$$

Where: C_i = total catch in year "i"
 \bar{C} = mean total catch over "n" years, and
 n = total number of years sampled.

This variance can be related to fluctuating year-class strength by noticing that the deviation for total catch equals the sum of the deviations by age for any given year "i". That is,

$$C_i - \bar{C} = \sum_{j=1}^k (c_{ij} - \bar{C}_j)$$

Where: c_{ij} = catch from age group "j" in year "i"
 \bar{C}_j = mean catch from age group "j" over "n" years,
 k = number of age groups in catch.

Substituting this expression of the deviation into equation (8) gives:

$$(9) \quad s^2 = \sum_{i=1}^n \left(\sum_{j=1}^k (c_{ij} - \bar{C}_j) \right)^2 / (n - 1)$$

The total deviations ($c_{ij} - \bar{C}_j$) for each cohort can be partitioned into three parts, the residual deviations transmitted at birth from an accumulation of past random disturbances in the cohort's parents (D_r), the random deviation from random disturbances acting directly on the cohort after birth (D_e), and the cohort's compensating response (D_c). The compensating response should always be opposite in sign to the net effect of the random deviations, because compensation acts to readjust the population to its equilibrium level. For example,

$$c_{ij} - \bar{C}_j = (D_r + D_e) - D_c$$

Using as an example the introduction of variation at the egg stage in the model, the sequence of events in forming the number of age 1 recruits was as follows:

- (1) Eggs were produced and deposited by the parent stock. The number of eggs deviated from the mean (or equilibrium value) due to the accumulated effects of disturbances from past years (D_r) in shaping the multi-aged parent stock.
- (2) A random environmental disturbance (D_e) altered the survival of the eggs or larvae, adding to or subtracting from the deviations transmitted at birth.
- (3) Between birth and age 1, density-dependent mortality (D_c) acted to readjust the net random deviations in

fry production ($D_r + D_e$) towards the equilibrium number of age-1 fish.

It would be difficult to actually measure and separate these different sources of variation in a real fishery. However, knowledge of such details helps one understand how variability can be affected by fishing or other factors.

In my model, the strength of the compensatory response was related to number of eggs produced at equilibrium and the coefficients of intraspecific competition, β_0 and β_1 . Combining the density dependent mortality functions (2) for both of the first 2 years of life gave a curve relating the production of age-1 recruits to the production of eggs (Fig. 7). Because of the mathematical similarities mentioned earlier, this curve was shaped like a Ricker stock-recruitment curve.

Mean egg production was inversely related to exploitation. For example, mean egg production was 130,000 per hectare for an unexploited population (point A, Fig. 7), 75,000 per hectare for a 229-mm size limit and a fishing rate of 1.0 (point B, Fig. 7), and 24,000 per hectare for a 120-mm size limit and a fishing rate of 0.7 (point C, Fig. 7). Because of the shape of this curve, the compensatory response was more variable at high or low egg production than at intermediate egg production. A deviation in egg number of $\pm 20\%$ produced a $\pm 5\%$ deviation in the number of age-1 fish at point A and a $\pm 8\%$ deviation at point C, but point B was near the flat dome in the curve, so the same deviation in egg numbers had almost no effect on numbers of age 1 at that point. This explains why the population was most stable at intermediate rates of exploitation (Fig. 5).

Production of age-1 fish from a given egg production is variable on the right of the dome (near point A) for a different reason than to the left of the dome (near point C). On the right, the population is highly stable and density-dependent mortality is stronger than needed to

adjust for the given level of random variation (that is, $D_r + D_e < D_c$). This causes the population to overshoot its equilibrium level after a disturbance, as for the simulations of the 254-mm size limit and the unexploited populations in Figure 4. On the left, the population is less stable and density-dependent mortality is not strong enough to completely adjust for random variation (that is, $D_r + D_e > D_c$). However, near the dome (point B), the strength of density-dependent mortality is on the average about equal to random variation (that is, $D_r + D_e = D_c$). These results are important because they demonstrate that highly stable populations can also be highly variable if their density-dependent response is strong enough to cause overshooting of equilibrium after a disturbance.

The other factor affecting the total variance of the catch was the number of age groups present. Increasing the number of age groups (k) tends to reduce the total variance (s^2) by reducing the value of the numerator in equation (9). This occurs because the probability that positive and negative deviations will cancel, when summed over an individual year, increases as the number of age groups increases. Expressed mathematically for a given year "i",

$$\lim_{k \rightarrow \infty} \left(\sum_{j=1}^k (c_{ij} - \bar{c}_j) \right) = 0$$

and thus,

$$\lim_{k \rightarrow \infty} (s^2) = 0.$$

The age structure effect on total variance has two important properties which should be recognized: first, younger, larger age groups will have greater weight than older, smaller ones; and second, the stabilizing effect of a large number of age groups will be more important when variability in year-class strength is high. As a consequence of the first property, changing fishing rate or

effort will have less effect on the stability of the catch than changing the minimum size of harvest (Fig. 6) because they impact on "opposite ends" of the age structure. Increasing fishing rate can reduce the number of older age groups through mortality, but the older age fish are few in number and have little effect on overall variability. A reduction in size limit can also reduce the number of older age groups through mortality, but in addition it usually increases the number of younger age groups in the catch. The younger age groups contain more fish and so have more weight in determining overall variability (see equation 9).

Catches in series 2 demonstrated that the age structure effect is more important for fisheries with widely fluctuating year-class strength (Fig. 6). Here, different trends in variability of the catch occurred for the two methods of introducing random variation. Variability of the catch increased as size limit increased for the age-1 method, while variability was minimal at intermediate size limits, changing little overall, for the egg method. The reason for these contrasting trends was the difference in magnitude of the year-class fluctuations. In the age-1 method, standard deviations were 48% to 50% of the means for individual age groups because random variation was introduced as cohorts entered the catch. In the egg method, deviations were only 11% to 12% of the means because density-dependent mortality acted after the random variation was introduced. Thus, the age-structure effect dominated the trends in the former case, and the density-dependent mortality effect dominated the trends in the latter case.

Discussion

Two aspects of my study had important implications for the ecology and management of fisheries. The first was the relationship between fishing regulations and the variability of age-structured populations and harvests. My model of a

stream brown trout population was least variable when exploited near maximum sustainable yield in weight. The primary basis for this result was the assumptions that environmental fluctuations had their primary effect on year-class strength and that density-dependent mortality in early life formed a dome-shaped stock-recruitment curve which regulated population size. As mentioned earlier, these assumptions are probably valid for many fish populations in temperate regions. However, caution should be used when extending the modeling results to the real world. Interactions from other population regulatory mechanisms, such as density-dependent growth, and complications from density related environmental factors, such as interspecific competition, were not considered in the model, and if these factors are significant in a fishery, they could change the relationship between variability and exploitation. Also, my results were obtained using constant fishing rates which do not in themselves generate population fluctuations as do constant-annual-quota regulations or variable fishing rates (Beddington and May 1977).

The stabilizing effect of age structure on the population and harvest is potentially important in any fishery with widely fluctuating year-class strength. Ecologists have shown that the evolution of age structure was probably necessary to ensure successful reproduction under fluctuating environmental conditions. Cole (1954) showed that a semelparous life history (a single breeding followed by death) was the optimum reproductive effort if environmental uncertainty was not considered. Murphy (1968) and Schaffer (1974) showed that uncertainty in survival from egg to first maturity and constant survival of adults generated selective pressure for an iteroparous life history (long life and repeated breeding), and for populations with discrete annual reproduction, this leads to discrete age groups. I extended these ideas on age structure to address the stability of harvest in a fishery as it relates to the

choice of managing via minimum size limits or effort restrictions. I showed that the variability of the catch does not necessarily reflect the variability of the population if their age structures differ and that fluctuations in annual catch are minimized by maintaining the lowest practical minimum size limit and managing the fishery by controlling fishing effort.

The second aspect of this study with important implications was the derivation of a new method of representing and interpreting the density-dependent mortality of juvenile salmonids. If my density-dependent mortality functions (2) accurately reflect the consequences of territoriality in early life, they lead to some interesting hypotheses regarding the population dynamics and management of salmonids in streams. For example, the Au Sable River contains exceptionally good spawning habitat, so it is no surprise that an unexploited brown trout population in the river would produce eggs to the right of the stock-recruitment dome. The biological interpretation of this might be that spawning success (fry production) for an unexploited population is greater than the carrying capacity of the river for juvenile trout. The converse may also be true, i.e., streams with shortages of spawning habitat may produce viable eggs (or fry) to the left of the dome, even when unexploited. Lack of suitable spawning habitat may reduce spawning success below the carrying capacity of the stream for juveniles. In such populations, exploitation would move egg production further to the left of the dome on the curve, and, hence, variability would increase and recruitment rate would decline. Also, empirical-stock-recruitment data for such a fishery would always form an asymptotic curve rather than a dome-shaped curve.

Another idea which follows from this line of reasoning involves the use of habitat by trout in a continuous but variable stream. Some of the density-dependent "mortality" observed in stream segments of limited length might actually

be density-dependent movement into and out of the segments. Thus, one function of the territoriality might be to promote dispersion of the young from areas in the stream with good spawning and nursery habitat to areas where spawning and nursery habitat are limited but conditions for the adults are good. In coastal streams, such dispersion of young might have been the driving force behind the evolution of anadromous behavior. The relationships between the habitat type, the success of reproduction, and the carrying capacities for various life stages are important and could be studied quantitatively in the context of my model.

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Table 1. Population parameters for brown trout in the Au Sable River, 1974 to 1979.

Item	Egg/1,000	Age group						
		0	1	2	3	4	5	6
<u>Mortality</u> ^a								
M	3.0843	0.2516	0.2614	0.4943	2.4080	1.6090	1.6090	2.3030
β	0.0137	0.0005	---	---	---	---	---	---
<u>Growth</u>								
Length in October (mm) ^b	---	96	167	232	292	347	399	446
<u>Reproduction</u>								
Percent females mature	---	0.0	14.4	77.8	96.8	100.0	100.0	100.0
Egg content	---	0	31	426	790	1,124	1,440	1,726

^a M = instantaneous natural mortality rate (density independent) and β = density-dependent mortality coefficient. See equations (1) and (2) in text.

^b (length in mm) = 1,033 {1-exp[-0.078 (age + 1.254)]}, where age = 0 represents fish at 6 months from hatching, age = 1 represents fish at 18 months from hatching, etc.

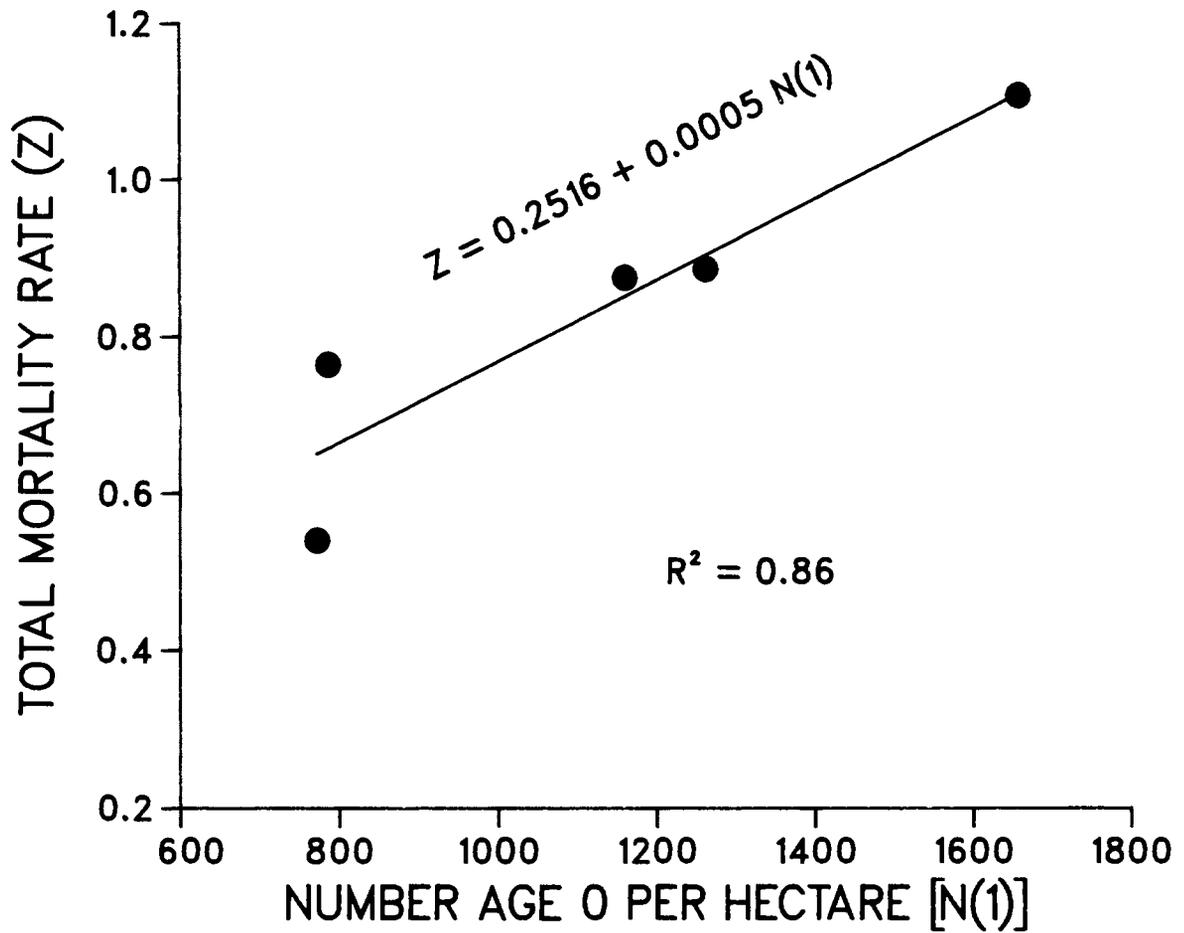


Figure 1. The relationship between the density of 6-month old brown trout (age-0) in the Mainstream Au Sable River and their mortality rate over the next year. Data were from annual population estimates conducted from 1974 to 1979.

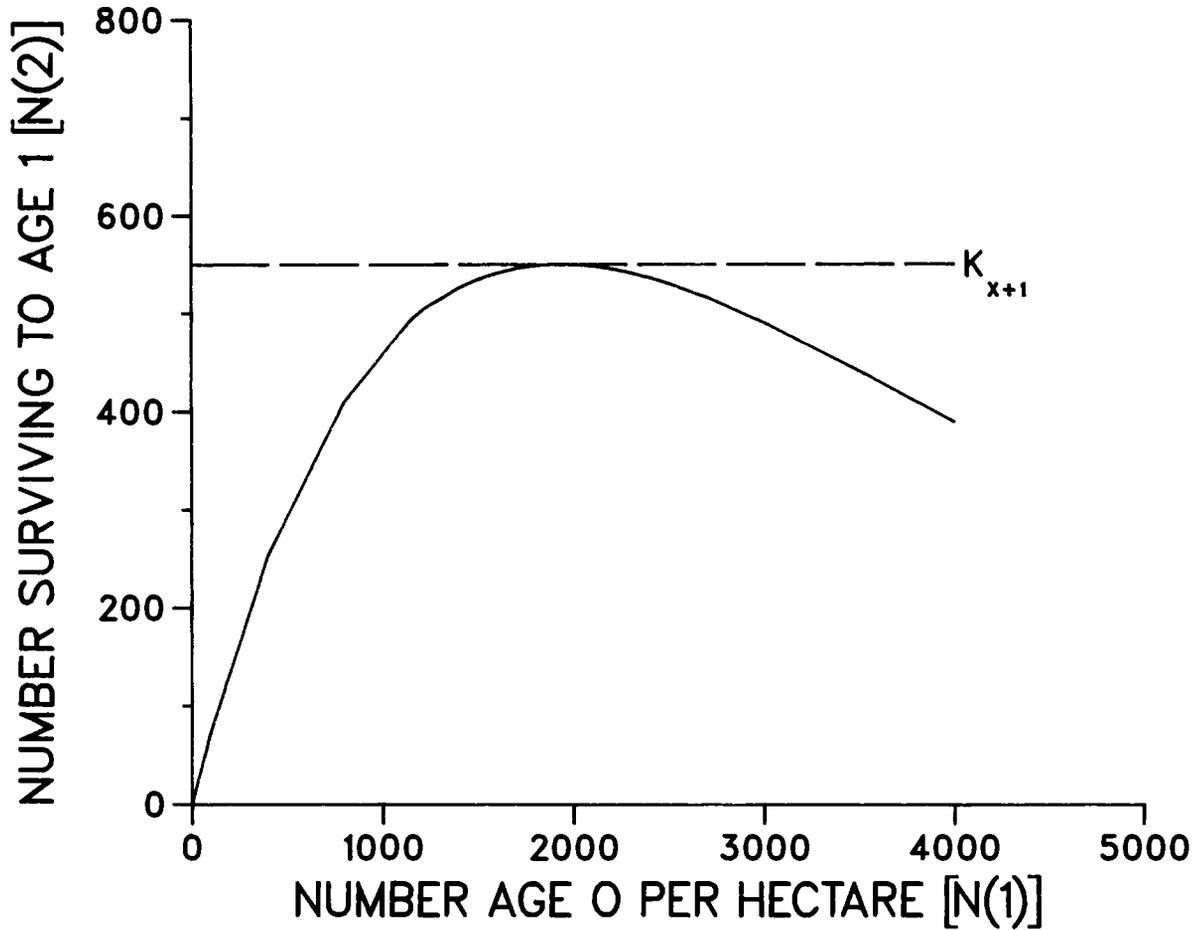


Figure 2. Predicted number of age-0 brown trout (6-month old) surviving to age 1 (18 months old) at different densities. The peak of the dome represents the effective carrying capacity (K_{x+1}) of the stream for age-1 brown trout.

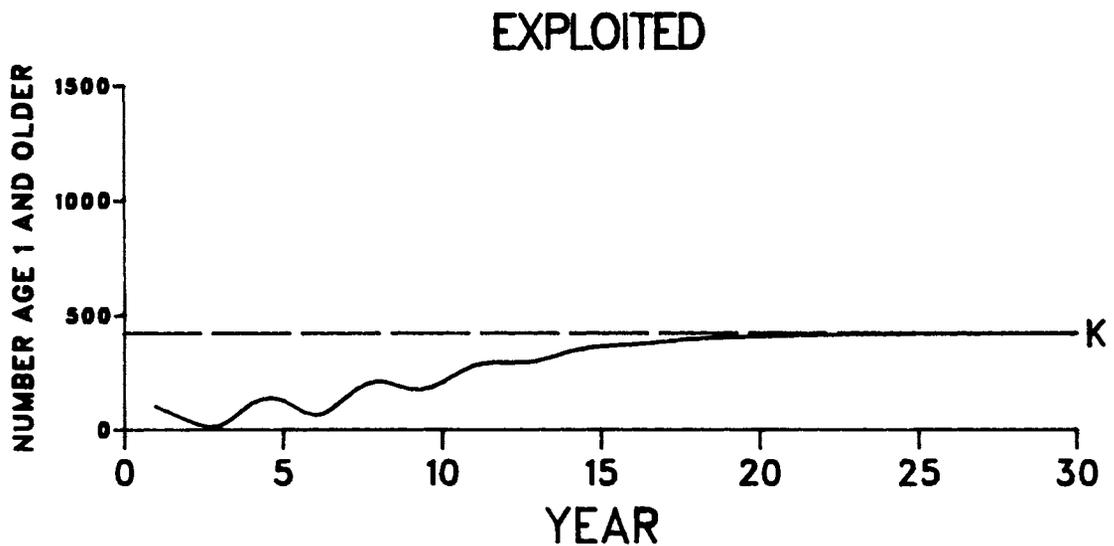


Figure 3. Trajectories of population growth (solid line) simulated for unexploited and exploited (size limit = 120 mm and $F = 0.7$) populations. The population equilibrium level is represented by K (dashed line).

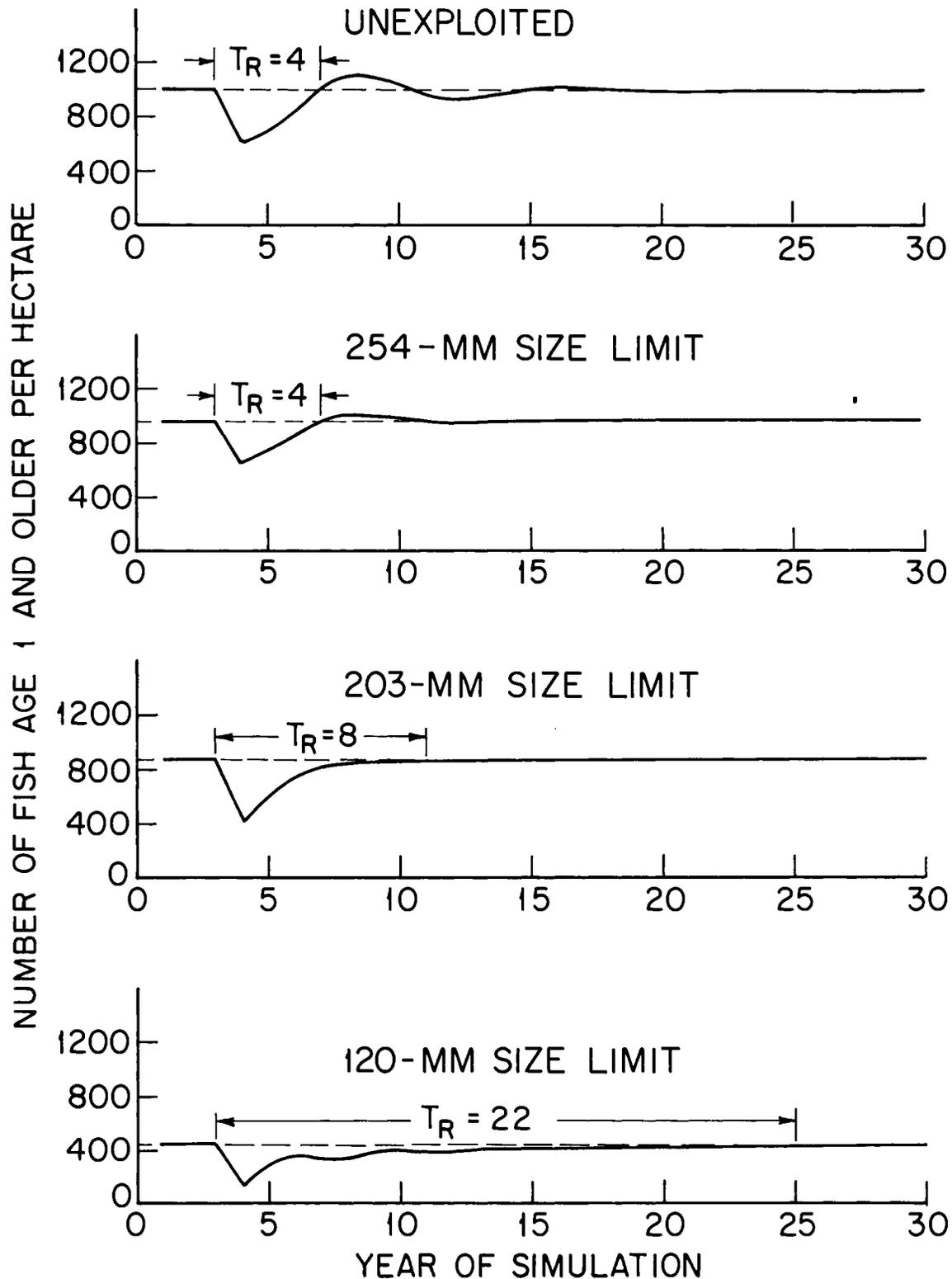
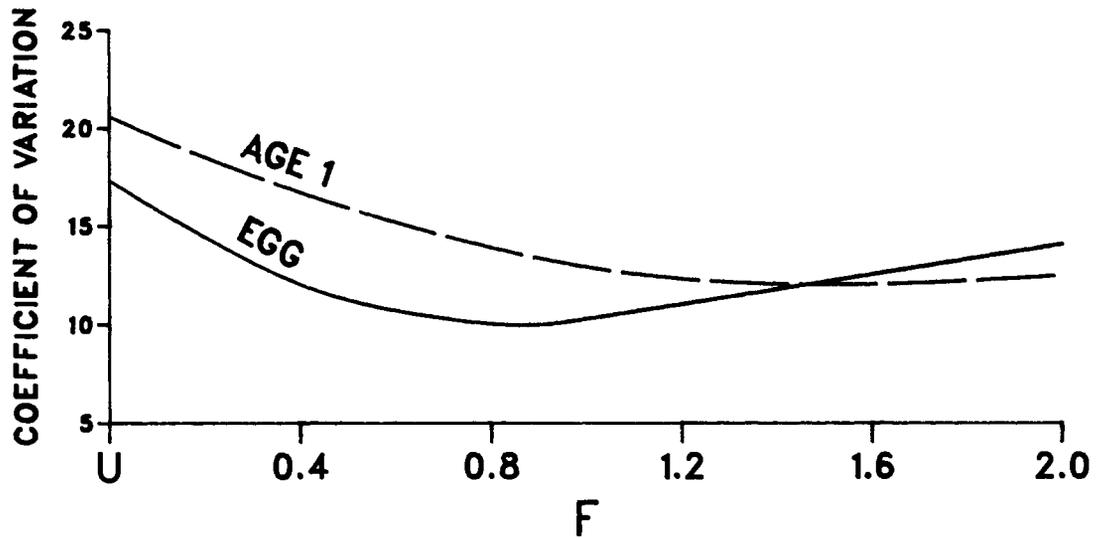


Figure 4. Population trajectories (solid line) showing the characteristic response times, T_R , after a 90% reduction of age-1 fish for four levels of exploitation. Dashed line represents equilibrium population size.

SIMULATION SERIES 1



SIMULATION SERIES 2

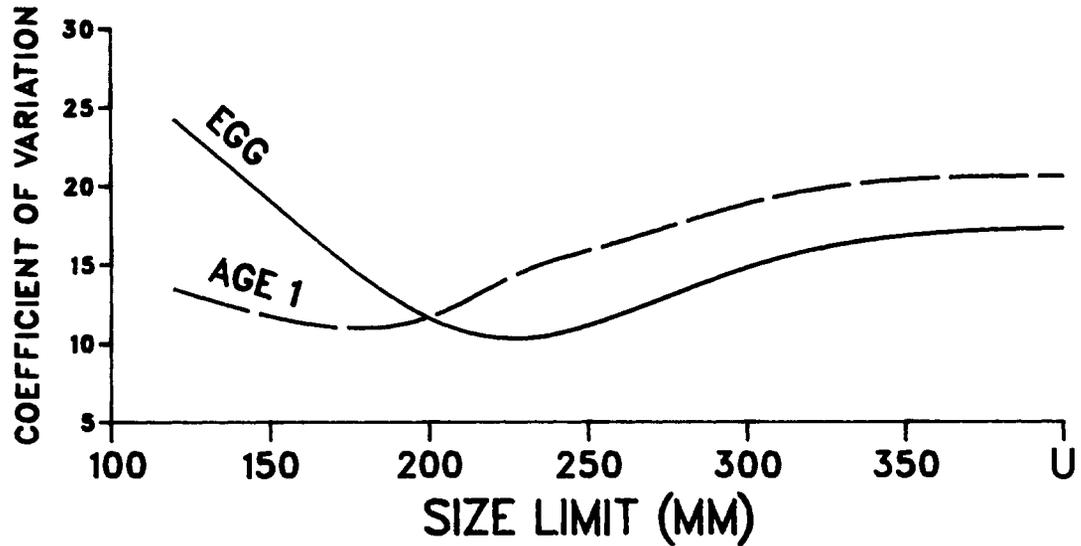


Figure 5. The relationship between the coefficient of variation of population size and: (1) the instantaneous fishing mortality rate at a 229-mm size limit (Simulation Series 1); and (2) the size limit at a 0.7 fishing rate (Simulation Series 2). Lines labeled "EGG" represent simulations in which random variation was introduced at the egg stage, while "AGE 1" represents simulations in which random variation was introduced at age 1. "U" on the horizontal axis represents unexploited populations.

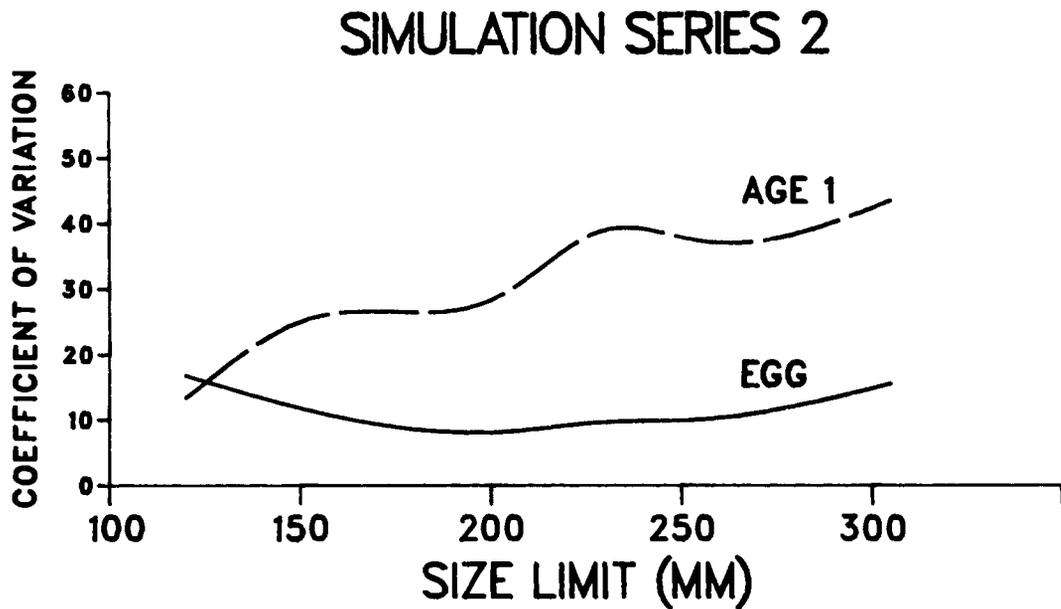
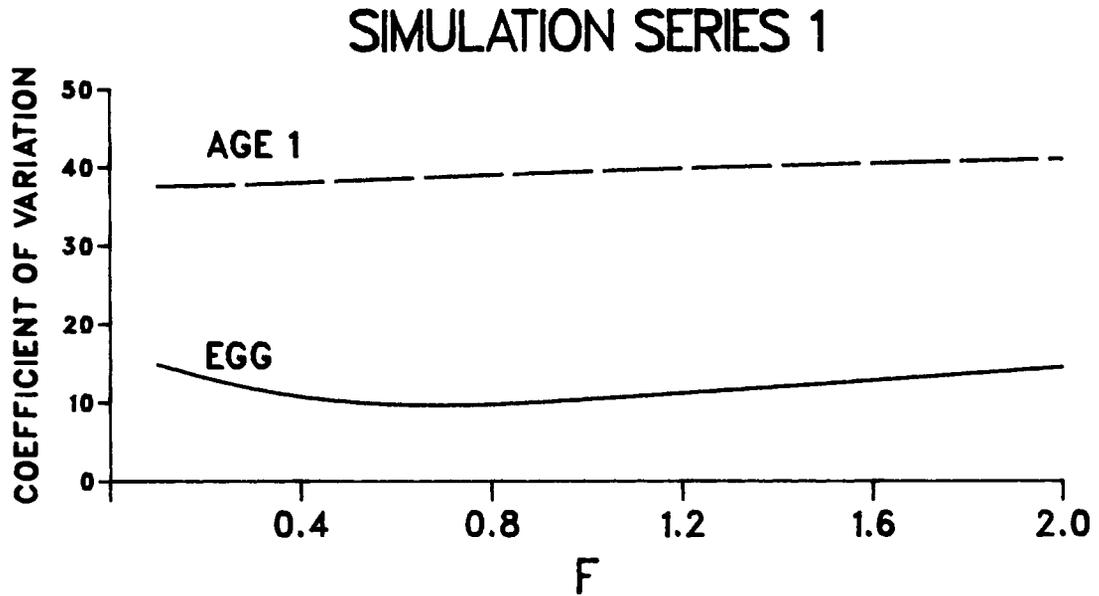


Figure 6. The relationships between the coefficient of variation of annual catch and: (1) the instantaneous fishing mortality rate at a 229-mm size limit (Simulation Series 1); and (2) the size limit at a 0.7 fishing rate (Simulation Series 2). Lines labeled "EGG" and "AGE 1" are same as for Figure 5.

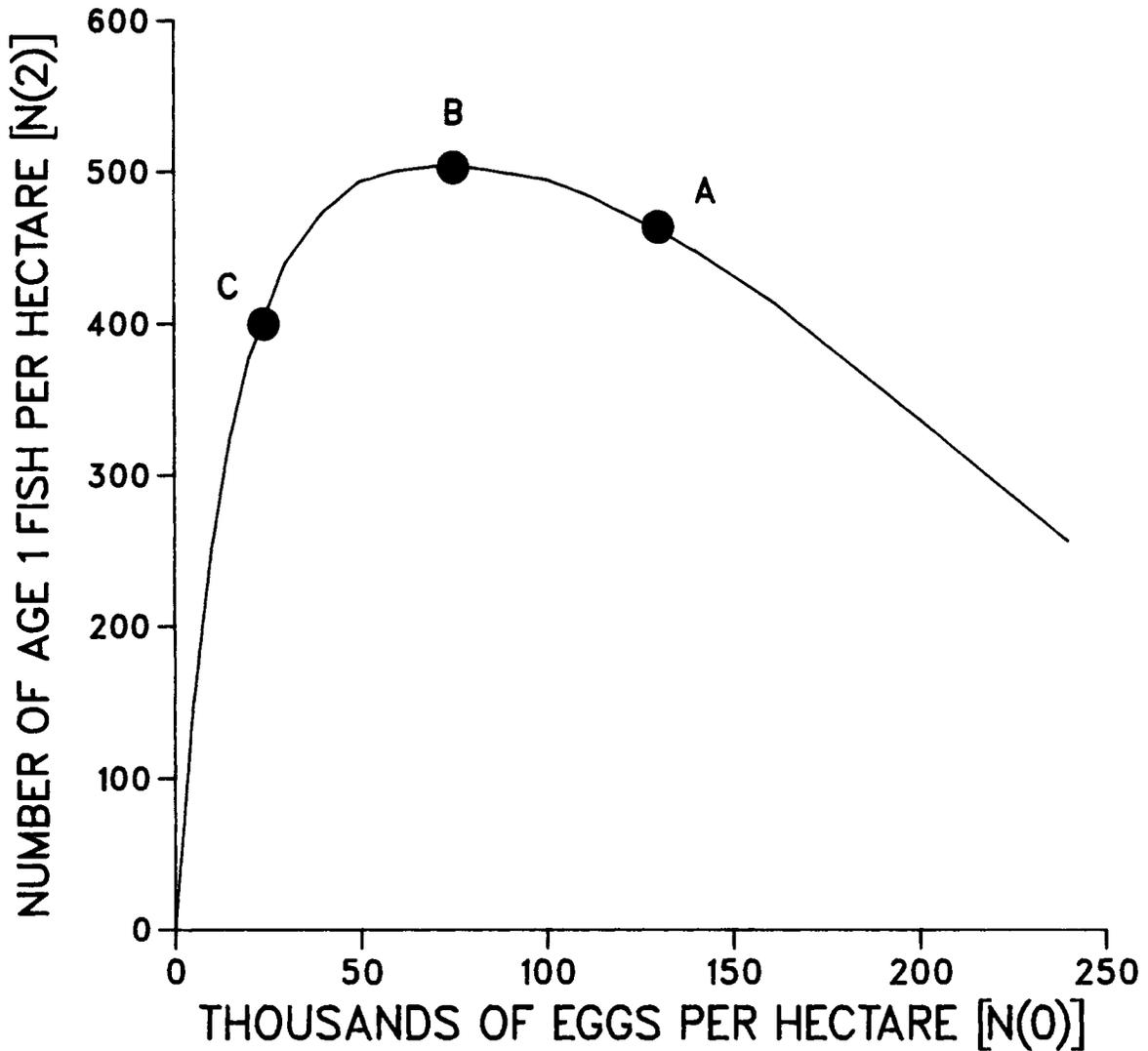


Figure 7. The relationship between the number of eggs surviving the 2 years from fall deposition and conception to fall of age 1 (18 months from hatching). Points A, B, and C represent the mean numbers of eggs and age-1 fish produced for simulations with no exploitation, a size limit of 229 mm and $F = 1.0$, and a size limit of 120 mm and $F = 0.7$, respectively.

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