

SOME MATHEMATICAL MODELS IN ECOLOGY

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SOME MATHEMATICAL MODELS IN ECOLOGY

BACKGROUND

Many people have studied population dynamics. Vito Volterra was one of the first people to study this subject. After World War I, it was assumed that the number of food fish in the Adriatic would be greater than before the war, since the population had not been exploited by fishing for several years. However it was found that the number of food fish (bottom fish) was smaller and the number of elasmobranchs which prey on the food fish, greatly increased. This situation aroused the interest of Vito Volterra. He set up systems of differential equations for the study of biological associations.

In his study of two species one of which feeds upon the other, he uses two differential equations.

$$\frac{dN_1}{dt} = (\epsilon_1 - \gamma_1 N_2) N_1$$

$$\frac{dN_2}{dt} = (-\epsilon_2 + \gamma_2 N_1) N_2$$

Here N_1 is the number of individuals in the prey species, and N_2 is the number of individuals in the predator species. ϵ_1 represents the coefficient of increase of the prey species if the predator species did not exist. ϵ_2 represents the coefficient of decrease of the predator species if the prey species did not exist, in which case it would suffer from lack of food. The coefficients γ_1 and γ_2

measure the aptitude of the prey species to defend itself and the means of offense of the predator species. $\frac{dN_1}{dt}$ and $\frac{dN_2}{dt}$ are the change in the populations N_1 and N_2 with respect to time (the first derivative of N_1 and N_2 with respect to time.)

By means of these equations, Volterra showed that there would be a periodic fluctuation of the number of individuals of the two species. He also showed that the averages of the numbers of individuals of the two species are constant so long as the coefficients of increase and decrease of the two species and those of protection and offense ($\epsilon_1, \epsilon_2, \delta_1, \delta_2$) remain constant.

In explaining the situation in the Adriatic, Volterra showed that if an attempt is made to destroy the individuals of the two species uniformly and in proportion to their number, the average of the number of individuals of the prey species decreases and the average of the number of individuals of the predator species increase.

In considering a biological association where two species compete for the same food, Volterra found that one species would be driven to extinction in that area. The differential equations which he used were:

$$\frac{dN_1}{dt} = [\epsilon_1 - \delta_1 (h_1 N_1 + h_2 N_2)] N_1$$

$$\frac{dN_2}{dt} = [\epsilon_2 - \delta_2 (h_1 N_1 + h_2 N_2)] N_2$$

Here ϵ_1 and ϵ_2 are the coefficients of increase, while δ_1 and δ_2 are the effects of competition for the same food

(overpopulation.) If $\frac{\epsilon_1}{\gamma_1} > \frac{\epsilon_2}{\gamma_2}$ the second species continually decreases and the number of individuals of the first species approaches $\frac{\epsilon_1}{\gamma_1 h_1}$ (8, p. 1-15, 19-27).

About the same time as Volterra was doing his work on population dynamics, Alfred J. Lotka was working on the same subject in the United States. Lotka's equations and methods for handling populations are essentially the same as Volterra's.

According to Lotka when one species eats members of two other species, it is possible for one of the two prey species to be exterminated. When the number of individuals of one of the prey species becomes small, the number of individuals of the predator species is not necessarily reduced since the second prey species may provide enough food. Thus the number of predators can be large even when the number of individuals of one species of prey is small. This situation may lead to the extermination of one species.

Lotka also studied growth and mortality curves of a single species, especially man. He showed that the age distribution of a species is variable, but only within somewhat restricted limits. With his equation he showed that the normal age distribution once established perpetuates itself, barring external change.

$$c(a) = b e^{-na} p(a)$$

$c(a)$ is the number of organisms in one age group (from a to $a + da$.)

$p(a)$ is the survival factor for that age group, $c(o) = b$, $b - d = r$ where d is the death rate per head. The normal age distribution, Lotka showed, will spontaneously return after being disturbed by a temporary change, such as a war in man (5, p. 94-95, 110-115).

Many objections to the mathematical models of Volterra and Lotka are given by H. G. Andrewartha and L. C. Birch. In considering a population composed of one species, they believe that the logistic theory, $(\frac{dN}{dt} = r_m N(1 - \frac{N}{K})$ where r_m is the innate capacity to increase) cannot be used unless the population has a stable age-distribution and this age-distribution is maintained. They feel that much of the experimental data on population growth cannot be directly interpreted by the logistic theory since a stable age-distribution was not obtained in the experiments.

In the case of two species competing in the same environment, Andrewartha and Birch wrote Volterra's equations in this form:

$$\begin{aligned}\frac{dN'}{dt} &= r'_m N' \left(1 - \frac{N' + \alpha N''}{K'}\right) \\ \frac{dN''}{dt} &= r''_m N'' \left(1 - \frac{N'' + \beta N'}{K''}\right).\end{aligned}$$

They consider this model unrealistic for the following reasons.

1. The assumptions of the logistic theory are repeated twice in this model.
2. The assumption is made that α and β are constants which

are independent of the numbers of each species.

3. The solution of the equations poses a biological situation which amounts to a contradiction. They claim that $N' + \alpha N''$ cannot be greater than K' which is its value when $\frac{dN'}{dt} = 0$ and N' reaches its asymptotic value after N'' approaches zero. Then, by using similar reasoning they make the statement that $N'' + \beta N'$ cannot be greater than K'' . With these two assumptions neither species can approach zero (2, p. 347-351, 407-412).

Gause cultured Paramecium aurelia and P. caudatum together, so that both were competing for the same food. P. caudatum eventually died out, leaving a dense population of P. aurelia (4, p. 97-113). Andrewartha and Birch say that in nature where space is not confining this situation is not likely to occur (2, p. 456-457).

A. J. Nicholson and V. A. Bailey, whose work will be discussed later, criticized the Lotka-Volterra prey-predator models on the following grounds.

1. Lotka and Volterra's equations seem to imply that the reaction when a predator encounters a prey is necessarily instantaneous. This objection, however, is taken care of in the fourth chapter of Volterra's book, Leçons sur la Théorie Mathématique de la Lutte Pour la Vie, where he uses integral-differential equations to handle the "time-lag" factor.

$$\frac{dN_1}{dt} = \left[\epsilon_1 - \delta_1 N_2(t) - \int_0^\infty F_1(t-\tau) N_2(\tau) d\tau \right] N_1(t) \quad 6$$

$$\frac{dN_2}{dt} = \left[-\epsilon_2 + \delta_2 N_1(t) + \int_0^\infty F_2(t-\tau) N_1(\tau) d\tau \right] N_2(t)$$

$$\epsilon_1, \epsilon_2, \delta_1, \delta_2, F_1, F_2 \geq 0$$

(8, p. 141-145).

2. It is implicit in the Lotka-Volterra models that each individual in the populations of prey and predator is exactly equivalent to every other individual of the same species.
3. Lotka and Volterra used the methods of calculus, which requires continuous change rather than discrete change (6, p. 551-552, 597-598).

Andrewartha and Birch state that the mere observation of oscillations in natural populations whether of prey or predator or both, provides no evidence of a causal relationship between predators and oscillations nor yet confirms either the premises or the conclusions of the mathematical models (2, p. 434).

A. J. Nicholson and V. A. Bailey also made a mathematical model for the study of biological populations. Their model is quite restrictive and only considers prey-predator situations where the predator lays eggs upon the prey. The prey is considered to be uniformly distributed over an area. Weather and food for the prey are held constant. It is assumed that the predator searches at random for the prey.

Later Nicholson and Bailey break their equations into year classes (generations), and use the methods of finite

differences. By doing this, they obtain oscillations in the population densities. They are also able to handle situations where three species are involved. The parasite has a parasite which in turn laid eggs upon it. They did not have the difficulties that Volterra had when he considered the interaction of an odd number of species. Volterra's conclusions will only hold when the number of prey species equals the number of predator species. Nicholson and Bailey believe that Volterra's difficulty arose from not considering the effect of age distribution (6, p. 551-555, 581-585, 590-592, 597-598) (8, p. 50-52).

Oliver P. Pearson made a mechanical model for studying population dynamics. The model is a long inclined plane into which a large number of holes have been drilled and down which balls are rolled. Three types of mortality can be considered in this model: proportional, compensatory, and density-independent. To achieve low rates of proportional mortality Tygon plastic bumpers were fitted on pegs behind each hole in such a way that a ball traveling by itself would not bounce readily into a hole. The tygon bumpers are replaced by rubber bumpers or the pegs are removed to simulate higher mortality rates. When several balls are rolled together, they may bump into each other and knock one or the other ball into a hole. Thus we have compensatory mortality. Density independent mortality is achieved by removing a certain number of balls

per unit time by hand.

If one of the balls comes safely through one "field" (a section of the board), it crosses a bronze strip which triggers the entrance of several more balls. This simulates reproduction. The board has five fields, thus five different age classes can be considered. Compensatory mortality and reproductive rates can be changed for each age class. Balls which reach the end of the board are put back at the beginning of the fifth field and can go through it again and again as long as they survive. A census of the population is made by a 35-mm. camera which periodically takes a picture of the board (7, p. 494-501).

Many other workers have applied the methods of mathematics to various phases of population dynamics. Fish and game management groups and forestry groups have typically been concerned with the effects of human predation upon a single prey species, and with determining the exploitation rate that will produce the maximum sustained yield from a given population of prey. In these fields, the mathematical treatment has been concerned mainly with the interaction between man, as a predator, and the exploitable adults of the species being studied.

Much recent work in ecology and oceanography has dealt with the passage of energy through a food chain composed of several different species. Here, rather than studying the numbers of organisms, the passage of energy

(food measured in calories) from one level of the food chain to the next is studied. Since the literature in both of the above fields is voluminous, and since the aims and approach differ more or less widely from those used in this study, no attempt will be made to review this work in detail.

Much work has been done in the study of the growth and development of populations consisting of one species. The field of demography studies the development of human populations. The term population does not necessarily mean the whole species. It can mean the inhabitants of one small, distinct area, or even more specifically just the members of one sex in an area.

Life tables are extremely useful in the study of human populations, especially actuarial work. The life table is a life history of a hypothetical group of people, as it is diminished gradually by death. This group is closed against immigration and emigration. It starts with a fixed group of births, say 1,000, 10,000, or 100,000; and follows this group through each year of its life recording the number of the original group surviving at each age. Except for the first year of life, it is assumed the deaths occur evenly throughout the year.

The information used in the construction of life tables is obtained from census figures and records of vital statistics. G. W. Barclay in his book on population

analysis discusses the reliability of this information and the techniques of making life tables. He also discusses the problem of determining human fertility. This is more difficult than studying fertility in animals since there is more of an element of choice in human reproductive rates (3, p. 5, 55-92, 93, 94, 11-115, 168-170).

In Principles of Animal Ecology, Allee, W. C. et al. give a rather complete discussion of population studies. They include all the major ideas discussed so far in this paper. However in applying the logistic curve to human populations, they expected the world population increase which began with the industrial revolution to begin leveling off in 1960. This of course did not happen. The human population boom seems to be advancing as rapidly as ever. This shows one of the dangers of extrapolation from data (1, p. 313-315).

METHODS AND PROCEDURES

Since interspecific relationships in nature are usually governed by a number of factors interacting in a complex way, any mathematical model that closely simulates nature is likely to involve a great deal of computation. Therefore, I used an Alvac III-E digital computer, which allowed me to perform rapidly many more arithmetic calculations than would have been possible otherwise. I was able to write rather elaborate programs. I have considered three different situations: the case of one species by itself; the case of two species and their interactions; and the case of three species which are allowed to interact with each other in several ways.

The Single-Species Model

First let us consider the changes in a one-species population over a period of time. The population is first divided into age classes. The notation $N_{i,j}$ is used to designate the number of organisms in the population which are i years old and were born in year j . The unit of time i , and j , could also be considered in weeks, days, or hours if this better fits the population to be studied. The number of young born in a particular year (j) is given by $N_{0,j}$. This is taken equal to

$$\sum_{i=1}^n K_i N_i^{j-i} = K_1 N_1^{j-1} + K_2 N_2^{j-2} + K_3 N_3^{j-3} + \dots + K_n N_n^{j-n},$$

where K_1 is the average number of offspring an i-year-old animal will produce in the i'th year, and where n is the maximum possible age attained by a member of this species. The K's can be either greater or less than one. The number of animals one year old or older present at a particular time can be expressed in terms of the number of animals of the same year class present the year before. Thus

$$N_i^j = N_{i-1}^j \left[f_{i-1} - c \sum_{a=0}^n N_a^{j+i-a-1} - p - g \right],$$

where N_i^j is the number of i-year-olds born in year j. N_{i-1}^j is the number of i-1-year-olds born in year j. (i.e. The number of members of the j'th year class alive last year.) f_{i-1} is the probability that an organism which has lived i-1 years will survive to the next year (the i'th year) under conditions of no predation or food deficiency and with a normal climate for the area.

$\sum_{a=0}^n N_a^{j+i-a-1}$ is the total number of organisms alive in the population in year $j + i - 1$. $\sum_{a=0}^n N_a^{j+i-a-1} = N_0^{j+i-1} + N_1^{j+i-2} +$

$$N_2^{j+i-3} + \dots + N_n^{j+i-n-1}$$

$c \sum_{a=0}^n N_a^{j+i-a-1}$ is the effect of overpopulation (compensatory mortality.) When the population is not too dense c will be taken as zero. If the population is very sparse so that the effects of underpopulation (depensatory mortality) appear, the term may be changed to $\frac{c'}{\sum_{a=0}^n N_a^{j+i-a-1}}$. p is

the reduction of the population by predators, and is a

function of the size of the predator population. g is the effect of the climate over the last year. This factor allows us to include the effect of extremes in the weather; drought, floods, hard winters, or by changing the sign even exceptionally favorable weather.

By use of a jump switch it is possible to put in a different factor for g (climate) each year. This factor can come from a table of random numbers. By moving another switch the machine will stop at the end of any year and changes may be typed into the program. Thus the rate of predation, the effects of over- or under-population, and the basic probability of an organism living to the next year can be changed. The numbers in the year classes can also be changed in this manner, thus introducing immigration, emigration, or density independent mortality.

The program was written so as to keep $\left[\frac{N_{i-1}}{N_i} - c \sum_{a=0}^m N_a^{j+i-a-1} - p - g \right]$ between zero and one. Since it is impossible for a negative number of organisms to be present, when this factor became negative, zero was substituted for it. Again when this factor became greater than one, one was substituted for it, since barring immigrations, it is impossible to have more members in the N_{i-1} class next year than there were in the N_i class this year. It may be argued that even under ideal conditions all the organisms in one year class would not live until the next year. By changing the

program slightly, it could be made so that all values of

$\left[f_{i-1} - c \sum_{a=0}^m N_a^{j+i-a-1} - p - g \right] \geq .95$ would be replaced by .95.

A Model for the Study of Two Species

The two-species model is similar to the one-species model. This model is in somewhat the same general form that Volterra used, but differs from the Volterra equations in that the populations are separated into age classes, and in that there is a factor for climate and a factor for a predator on the predator. Also, in contrast to Volterra's model, the changes are assumed to be discrete rather than continuous. The equations which were used are as follows:

$$(1) N_0^j = \sum_{i=1}^m K_i N_i^{j-i}$$

$$(2) N_i^j = N_{i-1}^j \left[f_{i-1} - c \sum_{a=0}^m N_a^{j+i-a-1} - d \sum_{a=0}^m M_a^{j+i-a-1} - g \right]$$

$$(3) M_0^j = \sum_{i=1}^m R_i M_i^{j-i}$$

$$(4) M_i^j = M_{i-1}^j \left[\bar{f}_{i-1} - \bar{c} \sum_{a=0}^m M_a^{j+i-a-1} + \bar{d} \sum_{a=0}^m N_a^{j+i-a-1} - \bar{g} - \bar{p} \right]$$

N	is the number of prey.
M	is the number of predators.
i	is the age of the organism.
j	is the year of birth of the organism.
N_0^j and M_0^j	are the number of young born in year j to the prey and predators respectively.

K_1 is the average number of offspring an i-year-old prey will produce in any given year.

$\bar{K}_1$ is the average number of offspring an i-year-old predator will produce in any given year.

f_{i-1} and $\bar{f}_{i-1}$ are the probabilities that an organism which has lived i-1 years will survive to the ith year, when prey-predator effects and climatic effects are not considered.

$c \sum_{a=0}^n N_a^{j+i-a-1}$ and $\bar{c} \sum_{a=0}^m M_a^{j+i-a-1}$ account for the effects of overpopulation.

n is the maximum possible age attained by the prey.

m is the maximum possible age attained by the predator.

$d \sum_{a=0}^m M_a^{j+i-a-1}$ is the effect of predation, which is directly related to the size of the predator population.

$\bar{d} \sum_{a=0}^n N_a^{j+i-a-1}$ is the effect of the food supply on the predator.

Possibly this last factor should be combined with the $\bar{f}$'s, or $\bar{d}$'s varied from positive to negative as the food varies from a mean value. This will of course depend on how large a factor this particular prey is in the survival of the predator. g is the effect of climate, and can be either positive or negative. $\bar{p}$ is the effect of a predator on the predator if there is one. This factor may or may not exist, and can also be dealt with by putting in a third animal.

The same general comments that apply to the one-species model still hold. Climate may be changed each year

by use of random numbers. The climate factor for the prey does not need to have the same value as the climate factor for the predator. These two factors may be the same, completely independent of each other, or have some relationship between these two extremes.

All the other factors in equations one to four may be changed at the end of each year (cycle). The factors

$$[f_{i-1} - c \sum_{a=0}^n N_a^{j+i-a-1} - d \sum_{a=0}^m M_a^{j+i-a-1} - g] \quad \text{and}$$

$$[\bar{f}_{i-1} - \bar{c} \sum_{a=0}^m M_a^{j+i-a-1} + \bar{d} \sum_{a=0}^n N_a^{j+i-a-1} - \bar{g} - \bar{p}]$$

are held between zero and one in the manner already discussed.

A Model for the Study of Three Species

The three-species model is a general model which can be used for many types of interactions between different species of organisms. It is written in such a way that more than three species could easily be added without changing the form. The basic equations are as follows:

$$(5) \quad L_0^j = \sum_{i=1}^l K_i L_i^{j-i}$$

$$(6) \quad L_i^j = L_{i-1}^j [f_{i-1} + c \sum_{a=0}^l L_a^{j+i-a-1} + d \sum_{a=0}^n N_a^{j+i-a-1} + e \sum_{a=0}^m M_a^{j+i-a-1} + p + g]$$

$$(7) \quad N_0^j = \sum_{i=1}^n \bar{K}_i N_i^{j-i}$$

$$(8) \quad N_i^j = N_{i-1}^j [\bar{f}_{i-1} + \bar{c} \sum_{a=0}^l L_a^{j+i-a-1} + \bar{d} \sum_{a=0}^n N_a^{j+i-a-1} + \bar{e} \sum_{a=0}^m M_a^{j+i-a-1} + \bar{p} + \bar{g}]$$

$$(9) M_0^j = \sum_{i=1}^m \bar{K} M_i^{j-i}$$

$$(10) M_i^j = M_{i-1}^j \left[\bar{f}_{i-1} + \bar{c} \sum_{a=0}^l L_a^{j+i-a-1} + \bar{d} \sum_{a=0}^n N_a^{j+i-a-1} + \bar{e} \sum_{a=0}^m M_a^{j+i-a-1} + \bar{p} + \bar{g} \right]$$

In equations 5 to 10, the notation resembles that for the previous situations; specifically the three species are divided into age classes. It is assumed that the period from i to $i-1$ is the same for all three species, but this period is not necessarily a year.

$$L_i^j, N_i^j, M_i^j$$

i is the "age" of the organism
 j is the "year" of birth of the organism.

$$L_0^j, N_0^j, M_0^j$$

indicate the number of young born in a particular "year" (time period), in each species.

$$K_1, \bar{K}_1, \bar{\bar{K}}_1$$

are the average number of offspring an i -year-old member of each species will produce during the given "year" (time period).

$$f_{i-1}, \bar{f}_{i-1}, \bar{\bar{f}}_{i-1}$$

are the probabilities that an organism which has lived $i-1$ "years" will survive to the i th "year", when the other factors such as $c \sum L$, $d \sum N$, $e \sum M$, p , and g are not considered. These factors allow for the effects of infant mortality and of higher death rates in older animals.

$$c, d, e$$

c is the effect of overpopulation or underpopulation of species L . d and e are the predation effect or beneficial effect of species N and M on species L . c , d , and e can be either positive or negative.

$$\bar{c}, \bar{d}, \bar{e}$$

$\bar{d}$ is the effect of overpopulation or underpopulation of species N . $\bar{c}$ and $\bar{e}$ are the predation effect or beneficial effect of species L and M on species N . $\bar{c}$, $\bar{d}$, and $\bar{e}$ can be either positive or negative.

$\bar{c}, \bar{d}, \bar{e}$	$\bar{e}$ is the effect of overpopulation or underpopulation of species M. c and d are the predation effect or beneficial effect of species L and N on species M. $\bar{c}, \bar{d},$ and $\bar{e}$ can be either positive or negative.
$p, \bar{p}, \bar{\bar{p}}$	represent the effect of predation other than that considered above, or exploitation by man.
$g, \bar{g}, \bar{\bar{g}}$	are factors for climatic effect. They can be positive or negative or changed yearly. $g, \bar{g},$ and $\bar{\bar{g}}$ are not necessarily equal.
l, n, m	are the maximum possible ages of individuals in species L, N, and M respectively.

The same general comments which were given for the other two species still hold. However if a prey-predator relation is such that one species has much effect on a second, but the second species has little effect on the first, then instead of using the factor $d \sum_{a=0}^m N_a^{j+i-a-1}$, the ratio $\frac{d \sum_{a=0}^m N_a^{j+i-a-1}}{\sum_{a=0}^l L_a^{j+i-a-1}}$ would be better

An example of this is the situation where a predator has more than enough food, so a change in the number of prey has little effect upon the population size of the predator. In this case the rate of predation would be proportional to the ratio of predator to prey. When the prey has a stronger effect on the size of the predator population, this effect is taken care of in equation eight where the size of the prey population affects the size of the predator population.

Climatic variations may be simulated by using random numbers. Any of the other factors can be easily changed at the end of each year (cycle) if so desired. If the p 's represent exploitation by man, the program may be modified so a different value of p is used for different age groups. This may be necessary, since man usually protects the young organisms from exploitation. The restriction that

$$[f_{i-1} + c \sum_{a=0}^l L_a^{j+i-a-1} + d \sum_{a=0}^n N_a^{j+i-a-1} + e \sum_{a=0}^m M_a^{j+i-a-1} + p + g],$$

$$[\bar{f}_{i-1} + \bar{c} \sum_{a=0}^l \bar{L}_a^{j+i-a-1} + \bar{d} \sum_{a=0}^n \bar{N}_a^{j+i-a-1} + \bar{e} \sum_{a=0}^m \bar{M}_a^{j+i-a-1} + \bar{p} + \bar{g}], \quad \text{and}$$

$$[\bar{\bar{f}}_{i-1} + \bar{\bar{c}} \sum_{a=0}^l \bar{\bar{L}}_a^{j+i-a-1} + \bar{\bar{d}} \sum_{a=0}^n \bar{\bar{N}}_a^{j+i-a-1} + \bar{\bar{e}} \sum_{a=0}^m \bar{\bar{M}}_a^{j+i-a-1} + \bar{\bar{p}} + \bar{\bar{g}}]$$

have values between zero and one inclusive, must also hold.

RESULTS

Single-Species Populations

Using the program for one species, I chose the following values for the different factors and initial values.

$N_0^0 = 100$	$f_0 = .65$	
$N_1^{-1} = 60$	$f_1 = .96$	$K_1 = .3$
$N_2^{-2} = 55$	$f_2 = .96$	$K_2 = .3$
$N_3^{-3} = 50$	$f_3 = .96$	$K_3 = .4$
$N_4^{-4} = 45$	$f_4 = .90$	$K_4 = .4$
$N_5^{-5} = 40$	$f_5 = .80$	$K_5 = .4$
$N_6^{-6} = 30$	$f_6 = .70$	$K_6 = .3$
$N_7^{-7} = 20$	$f_7 = .50$	$K_7 = .2$
$N_8^{-8} = 10$	$f_8 = .30$	$K_8 = .1$
$N_9^{-9} = 2$	$f_9 = .10$	$K_9 = 0$
$N_{10}^{-10} = 0$	$f_{10} = 0$	$K_{10} = 0$
$\Sigma N = 412$		
$c = .001$	$p = .002$	$g = .0003$

Without making changes in any factor, the program was allowed to run for 198 cycles (years). It reached a steady population of 498.5, with very little variation from this value (Figure I). The age classes in this stable population are given in Table I.

Table I

N_0^{198}	=	123	N_6^{192}	=	35
N_1^{197}	=	74	N_7^{191}	=	23
N_2^{196}	=	67	N_8^{190}	=	10
N_3^{195}	=	61	N_9^{189}	=	2.5
N_4^{194}	=	55	N_{10}^{188}	=	0
N_5^{193}	=	47			

Using this stable population, the value of the f 's were changed to simulate an epidemic. The new values for the f 's were:

f_0	=	.33	f_6	=	.35
f_1	=	.48	f_7	=	.25
f_2	=	.48	f_8	=	.15
f_3	=	.48	f_9	=	.05
f_4	=	.45	f_{10}	=	0
f_5	=	.40			

After two cycles (years) with the f 's at these values, they were returned to their original values. At the end of the second cycle the population reached a minimum of 117. Then it gradually returned to its original value of 498. After 86 cycles the population size was 493 (Figure II).

Next, 500 individuals were placed in the zero year class to simulate the development of a population placed in a virgin territory. The factors for climate, predation,

probability of survival of each year class, and overpopulation were the same as in the first situation. The population reached a low of 387 the first cycle. Then it rose to a maximum of 609 in the fifth cycle. From there the population gradually returned to the stable size of 498.5. It was 498.97 after 82 cycles (Figure III). The population decreased from the fifth to the ninth cycle and then maintained approximately the same value of 562 and 561 in cycles nine, ten, and eleven. This plateau is due to the larger number of "births" in cycles four and five which have now reached the older age groups and which act to retard the gradual decrease of the total population (Figure IV).

The values of g were then varied by use of random numbers while everything else was held in the stable condition of the first situation. This, of course, caused the population size to oscillate irregularly.

Interactions Between Two Species

In the two-species model, there was a damped oscillation in the number of prey organisms and the number of predator organisms (Figure V). In this case the constants in Table II were used.

Table II

<u>Prey</u>		<u>Predator</u>	
c_n	= .0001	$\bar{c}_m$	= .0001
d_n	= .0003	$\bar{d}_m$	= .0003
e_n	= .0003	$\bar{e}_m$	= .0003
		$\bar{p}_m$	= .002
K_1	= 1.2	$\bar{K}_1$	= .3
K_2	= 1.2	$\bar{K}_2$	= .3
K_3	= 1.6	$\bar{K}_3$	= .4
K_4	= 1.6	$\bar{K}_4$	= .4
K_5	= 1.6	$\bar{K}_5$	= .4
K_6	= 1.2	$\bar{K}_6$	= .3
K_7	= .8	$\bar{K}_7$	= .2
K_8	= .4	$\bar{K}_8$	= .1
K_9	= 0	$\bar{K}_9$	= 0
K_{10}	= 0	$\bar{K}_{10}$	= 0
f_0	= .75	$\bar{f}_0$	= .3
f_1	= .98	$\bar{f}_1$	= .5
f_2	= .98	$\bar{f}_2$	= .5
f_3	= .98	$\bar{f}_3$	= .5
f_4	= .97	$\bar{f}_4$	= .5
f_5	= .92	$\bar{f}_5$	= .4
f_6	= .9	$\bar{f}_6$	= .3
f_7	= .8	$\bar{f}_7$	= .2
f_8	= .1	$\bar{f}_8$	= .7
f_9	= .05	$\bar{f}_9$	= .3
f_{10}	= 0	$\bar{f}_{10}$	= 0

When the values for d_n and $\bar{d}_m$ were smaller the fluctuations were smaller, and if d_n and $\bar{d}_m$ were small enough no fluctuations occurred. Whenever the values for the $\bar{f}_m$'s were larger, this species did not show oscillation. Such a situation occurred when the $\bar{f}_m$'s were taken as

$\bar{f}_0 = .3$	$\bar{f}_6 = .4$
$\bar{f}_1 = .6$	$\bar{f}_7 = .2$
$\bar{f}_2 = .6$	$\bar{f}_8 = .1$
$\bar{f}_3 = .6$	$\bar{f}_9 = .05$
$\bar{f}_4 = .6$	$\bar{f}_{10} = 0$
$\bar{f}_5 = .5$	

and the values of d_n and $\bar{d}_m$ were both .0001. In this case neither species showed oscillation, but both level off at a steady value for each species. The effect of climate as a random factor was then studied.

Starting with the same values as were used for Figure V, the program was allowed to go through four cycles before changing the climate. From then on, for each cycle a different number was used for g_n and $\bar{g}_m$. Numbers were obtained from a table of random numbers and were coded in the following way.

Number	Value for g_n or $\bar{g}_m$
0	0
1	.001
2	.002
3	.004
4	.008
5	-.001
6	-.002
7	-.004
8	-.008

The number nine was skipped. The first number was used for the prey species, g_n ; the second number was for the predator species, $\bar{g}_m$. The third number was used in the next cycle for the prey, and so on. As can easily be seen in Figure VI, the fluctuations are more erratic and are not damped as they are in Figure V. (Cycle 2 in Figure V corresponds to cycle 1 in Figure VI. i.e. The time numbers in Figure VI need to be moved one to the right to correspond exactly with Figure V.)

Next the case where two species compete for the same food was examined. The factors and initial values in Table III were used.

Table III

First Species

$$\begin{aligned}c_n &= .0001 \\d_n &= .0001 \\g_n &= 0\end{aligned}$$

$$N_0^0 = 765$$

$$N_1^{-1} = 258$$

$$N_2^{-2} = 146$$

$$N_3^{-3} = 83$$

$$N_4^{-4} = 46$$

$$N_5^{-5} = 26$$

$$N_6^{-6} = 14$$

$$N_7^{-7} = 7$$

$$N_8^{-8} = 2$$

$$N_9^{-9} = 1$$

$$N_{10}^{-10} = 0$$

$$K_1 = 1.2$$

$$K_2 = 1.2$$

$$K_3 = 1.6$$

$$K_4 = 1.6$$

$$K_5 = 1.6$$

$$K_6 = 1.2$$

$$K_7 = .8$$

$$K_8 = .4$$

$$K_9 = 0$$

$$K_{10} = 0$$

Second Species

$$\begin{aligned}\bar{c}_m &= .00005 \\ \bar{d}_m &= .0002 \\ \bar{g}_m &= 0 \\ p_m &= 0\end{aligned}$$

$$M_0^0 = 750$$

$$M_1^{-1} = 300$$

$$M_2^{-2} = 150$$

$$M_3^{-3} = 90$$

$$M_4^{-4} = 60$$

$$M_5^{-5} = 40$$

$$M_6^{-6} = 20$$

$$M_7^{-7} = 10$$

$$M_8^{-8} = 3$$

$$M_9^{-9} = 1$$

$$M_{10}^{-10} = 0$$

$$\bar{K}_1 = .8$$

$$\bar{K}_2 = .8$$

$$\bar{K}_3 = .9$$

$$\bar{K}_4 = .8$$

$$\bar{K}_5 = .7$$

$$\bar{K}_6 = .6$$

$$\bar{K}_7 = .5$$

$$\bar{K}_8 = .4$$

$$\bar{K}_9 = 0$$

$$\bar{K}_{10} = 0$$

Table III - continued

<u>First Species</u>	<u>Second Species</u>
$f_0 = .65$	$\bar{f}_0 = .75$
$f_1 = .8$	$\bar{f}_1 = .9$
$f_2 = .8$	$\bar{f}_2 = .9$
$f_3 = .85$	$\bar{f}_3 = .9$
$f_4 = .8$	$\bar{f}_4 = .9$
$f_5 = .8$	$\bar{f}_5 = .8$
$f_6 = .6$	$\bar{f}_6 = .6$
$f_7 = .4$	$\bar{f}_7 = .4$
$f_8 = .2$	$\bar{f}_8 = .3$
$f_9 = .1$	$\bar{f}_9 = .1$
$f_{10} = 0$	$\bar{f}_{10} = 0$

Since $\bar{d}_m$ is negative, an increase in the size of the population of species one has a negative effect on species two; as also an increase in the size of species two has a negative effect on species one. In this situation the population of species two went from 1424 individuals to zero individuals in 16 cycles (Table IV).

The value of c_n was changed to .00015 and of d_n to .00015, and everything else kept as it was above. This time the size of the population of the first species went from 1325 individuals to 4 individuals in 13 cycles (Table V).

Next, the value of d_n was changed to .0001 and the other factors kept as they were in the second case. Now

Table IV

<u>Cycle</u>	<u>First Species</u>	<u>Second Species</u>
0	1325	1424
1	1362	1190
2	1435	1053
3	1602	829
4	1735	681
5	1878	536
6	2039	400
7	2197	280
8	2355	184
9	2491	112
10	2593	63
11	2675	34
12	2746	11
13	2769	5
14	2780	3
15	2786	1
16	2790	0

Table V

<u>Cycle</u>	<u>First Species</u>	<u>Second Species</u>
0	1325	1424
1	924	1191
2	774	1316
3	713	1408
4	651	1523
5	583	1667
6	506	1848
7	422	2070
8	277	2528
9	187	2885
10	110	3288
11	52	3722
12	18	4146
13	4	missing

the population of species two went from $142\frac{1}{2}$ individuals to 92 individuals in 27 cycles (Table VI). The number of individuals in species two formed a monotonic decreasing sequence of terms with each one smaller than the one before.

This seems to indicate that it would be very difficult to get two ecologically similar species to survive together in the same environment, since slight changes in the factors for the relationships between the two species will tip the balance and cause one species or the other to go to extinction. To find a set of values so that they would both survive would be quite difficult. These values would have very narrow limits within which both species would survive. This type of situation would be very unlikely to occur in nature.

Interactions among Three Species

In the first three-species situation species L was eaten by species N and species M, while species M also ate species N. The factors and initial values of Table VII were used.

In this case the sign is important, since all factors are assumed positive unless there is a negative sign. Damped oscillations were obtained in all three species, as shown in Figure VII.

Table VI

<u>Cycle</u>	<u>First Species</u>	<u>Second Species</u>
0	1325	1424
1	1141	1191
2	1111	1141
3	1105	1113
4	1109	1088
5	1119	1062
6	1132	1031
7	1166	967
8	1199	910
9	1219	871
10	1260	805
11	1302	733
12	1334	686
13	1366	637
14	1398	587
15	1432	537
16	1467	486
17	1502	436
18	1537	389
19	1568	343
20	1605	300
21	1636	259
22	1665	223
23	1692	189
24	1717	160
25	1736	134
26	1758	111
27	1776	92

Table VII

<u>Species L</u>	<u>Species N</u>	<u>Species M</u>
$c_1 = -.0001$	$\bar{c}_n = .0003$	$\bar{\bar{c}}_m = .0001$
$d_1 = -.0003$	$\bar{d}_n = -.0001$	$\bar{\bar{d}}_m = .0003$
$e_1 = -.0001$	$\bar{e}_n = -.0002$	$\bar{\bar{e}}_m = -.0001$
$p_1 = 0$	$\bar{p}_n = 0$	$\bar{\bar{p}}_m = -.003$
$g_1 = .002$	$\bar{g}_n = -.001$	$\bar{\bar{g}}_m = -.002$
$L_0^0 = 847$	$N_0^0 = 203$	$M_0^0 = 200$
$L_1^{-1} = 290$	$N_1^{-1} = 134$	$M_1^{-1} = 115$
$L_2^{-2} = 164$	$N_2^{-2} = 115$	$M_2^{-2} = 85$
$L_3^{-3} = 92$	$N_3^{-3} = 98$	$M_3^{-3} = 50$
$L_4^{-4} = 52$	$N_4^{-4} = 85$	$M_4^{-4} = 20$
$L_5^{-5} = 29$	$N_5^{-5} = 73$	$M_5^{-5} = 5$
$L_6^{-6} = 15$	$N_6^{-6} = 56$	$\Sigma M = 475$
$L_7^{-7} = 7$	$N_7^{-7} = 37$	
$L_8^{-8} = 3$	$N_8^{-8} = 20$	
$L_9^{-9} = 1$	$N_9^{-9} = 9$	
$L_{10}^{-10} = 0$	$N_{10}^{-10} = 4$	
$\Sigma L = 1500$	$\Sigma N = 834$	
$K_1 = 1.2$	$\bar{K}_1 = .3$	$\bar{\bar{K}}_1 = .8$
$K_2 = 1.2$	$\bar{K}_2 = .3$	$\bar{\bar{K}}_2 = 1$
$K_3 = 1.6$	$\bar{K}_3 = .4$	$\bar{\bar{K}}_3 = .8$
$K_4 = 1.6$	$\bar{K}_4 = .4$	$\bar{\bar{K}}_4 = .4$
$K_5 = 1.6$	$\bar{K}_5 = .4$	$\bar{\bar{K}}_5 = 0$

Table VII - continued

<u>Species L</u>	<u>Species N</u>	<u>Species M</u>
$K_6 = 1.2$	$\overline{K}_6 = .3$	
$K_7 = .8$	$\overline{K}_7 = .2$	
$K_8 = .4$	$\overline{K}_8 = .1$	
$K_9 = 0$	$\overline{K}_9 = 0$	
$K_{10} = 0$	$\overline{K}_{10} = 0$	
$f_0 = .75$	$\overline{f}_0 = .3$	$\overline{\overline{f}}_0 = .35$
$f_1 = .95$	$\overline{f}_1 = .5$	$\overline{\overline{f}}_1 = .5$
$f_2 = .95$	$\overline{f}_2 = .5$	$\overline{\overline{f}}_2 = .5$
$f_3 = .95$	$\overline{f}_3 = .5$	$\overline{\overline{f}}_3 = .3$
$f_4 = .95$	$\overline{f}_4 = .5$	$\overline{\overline{f}}_4 = .2$
$f_5 = .92$	$\overline{f}_5 = .4$	$\overline{\overline{f}}_5 = 0$
$f_6 = .9$	$\overline{f}_6 = .3$	
$f_7 = .8$	$\overline{f}_7 = .2$	
$f_8 = .7$	$\overline{f}_8 = .1$	
$f_9 = .3$	$\overline{f}_9 = .05$	
$f_{10} = 0$	$\overline{f}_{10} = 0$	

Next the reproductive rates of the predator species M were changed to $\overline{\overline{K}}_1 = .4$

$$\overline{\overline{K}}_2 = .5$$

$$\overline{\overline{K}}_3 = .4$$

$$\overline{\overline{K}}_4 = .2$$

$$\overline{\overline{K}}_5 = 0$$

and all the other factors left the same as in the former situation. In this case species M went to extinction. After 112 cycles there were five organisms left, whereas in the former situation the number of organisms in species M oscillated about 1100 organisms. Species N averaged about 830 organisms, while in the previous example it had varied around 280 organisms. Species L fluctuated around 1480 individuals, while in the first case its eventual value was around 2000. Thus the presence of species M kept the population of species N low and allowed species L to reach a higher value. This outcome makes good sense, since the program was arranged to make the predation of species N greater on species L than the predation of species M (Figures VII and VIII).

The next situation considered was that in which one predator, species M, eats two prey, species L and N. There is no relationship between the number of individuals in species L and N. The factors and initial values which were used are given in Table VIII.

Table VIII

<u>Species L</u>	<u>Species N</u>	<u>Species M</u>
$c_1 = .0002$	$\bar{c}_n = 0$	$\bar{c}_m = .0001$
$d_1 = 0$	$\bar{d}_n = -.0001$	$\bar{d}_m = .0002$
$e_1 = -.0003$	$\bar{e}_n = -.0002$	$\bar{e}_m = -.0003$
$p_1 = 0$	$\bar{p}_n = 0$	$\bar{p}_m = 0$
$g_1 = 0$	$\bar{g}_n = .001$	$\bar{g}_m = -.001$
$L_0^0 = 847$	$N_0^0 = 424$	$M_0^0 = 212$
$L_1^{-1} = 290$	$N_1^{-1} = 150$	$M_1^{-1} = 75$
$L_2^{-2} = 164$	$N_2^{-2} = 82$	$M_2^{-2} = 41$
$L_3^{-3} = 92$	$N_3^{-3} = 50$	$M_3^{-3} = 25$
$L_4^{-4} = 52$	$N_4^{-4} = 25$	$M_4^{-4} = 13$
$L_5^{-5} = 29$	$N_5^{-5} = 15$	$M_5^{-5} = 8$
$L_6^{-6} = 15$	$N_6^{-6} = 7$	$M_6^{-6} = 4$
$L_7^{-7} = 7$	$N_7^{-7} = 3$	$M_7^{-7} = 3$
$L_8^{-8} = 3$	$N_8^{-8} = 2$	$M_8^{-8} = 2$
$L_9^{-9} = 1$	$N_9^{-9} = 1$	$M_9^{-9} = 1$
$L_{10}^{-10} = 0$	$N_{10}^{-10} = 0$	$M_{10}^{-10} = 0$
$\Sigma L = 1500$	$\Sigma N = 759$	$\Sigma M = 384$
$K_1 = 1.4$	$\bar{K}_1 = .7$	$\bar{K}_1 = .4$
$K_2 = 1.8$	$\bar{K}_2 = .9$	$\bar{K}_2 = .5$
$K_3 = 2$	$\bar{K}_3 = 1$	$\bar{K}_3 = .5$
$K_4 = 2$	$\bar{K}_4 = 1$	$\bar{K}_4 = .5$
$K_5 = 1.8$	$\bar{K}_5 = .9$	$\bar{K}_5 = .5$

Table VIII - continued

<u>Species L</u>	<u>Species N</u>	<u>Species M</u>
$K_6 = 1.4$	$\bar{K}_6 = .7$	$\bar{\bar{K}}_6 = .4$
$K_7 = .9$	$\bar{K}_7 = .5$	$\bar{\bar{K}}_7 = .3$
$K_8 = .5$	$\bar{K}_8 = .3$	$\bar{\bar{K}}_8 = .2$
$K_9 = .2$	$\bar{K}_9 = .1$	$\bar{\bar{K}}_9 = .1$
$K_{10} = 0$	$\bar{K}_{10} = 0$	$\bar{\bar{K}}_{10} = 0$
$f_0 = .6$	$\bar{f}_0 = .75$	$\bar{\bar{f}}_0 = .3$
$f_1 = .95$	$\bar{f}_1 = .9$	$\bar{\bar{f}}_1 = .5$
$f_2 = .95$	$\bar{f}_2 = .9$	$\bar{\bar{f}}_2 = .5$
$f_3 = .95$	$\bar{f}_3 = .9$	$\bar{\bar{f}}_3 = .5$
$f_4 = .95$	$\bar{f}_4 = .9$	$\bar{\bar{f}}_4 = .5$
$f_5 = .92$	$\bar{f}_5 = .9$	$\bar{\bar{f}}_5 = .4$
$f_6 = .9$	$\bar{f}_6 = .9$	$\bar{\bar{f}}_6 = .3$
$f_7 = .8$	$\bar{f}_7 = .8$	$\bar{\bar{f}}_7 = .2$
$f_8 = .7$	$\bar{f}_8 = .7$	$\bar{\bar{f}}_8 = .1$
$f_9 = .3$	$\bar{f}_9 = .3$	$\bar{\bar{f}}_9 = .05$
$f_{10} = 0$	$\bar{f}_{10} = 0$	$\bar{\bar{f}}_{10} = 0$

Lotka reported that it was possible for one prey species to go to extinction in this type of situation. Neither of the prey species in this program became extinct, but they do have rather violent fluctuations. If Figure IX is studied closely, it will be seen that the size of species M increases after species L and/or species N become large. When the size of species L and N is small, the population of species M immediately decreases. The many large fluctuations seem to indicate that this population structure is not very stable and that one species could become extinct rather easily.

FURTHER DEVELOPMENTS AND COMMENTS

The three-species model can easily be extended to include any number of species. The only limit is the memory size of the computer. On the Alvac III-E there is room to store at least 20 species. The general form of the three-species model would be used.

$$N_i = N_{i-1} [f_{i-1} + a_1 \sum N_1 + a_2 \sum N_2 + a_3 \sum N_3 + a_4 \sum N_4 + \dots + a_n \sum N_n + p + g]$$

constitutes a general form of the equations. Here N_1 stands for the first species, not an age group, N_2 stands for the second species, and so forth. The types of relationships between any two species would be determined by the size and sign of the a 's.

If two or more organisms reproduce at different intervals this situation can also be handled. Assume one organism has three litters per year while another has only one. The program could be so coded that the computer would go through three cycles for the first species each time it went through one cycle for the second. To consider a more complex case, let us assume one species has three litters per year while another has two. In this case the numbers three and two would be placed so that on each cycle they would be reduced by one. When one of these numbers became zero the computer would calculate the population of the species corresponding to that number and replace the zero with a three or two.

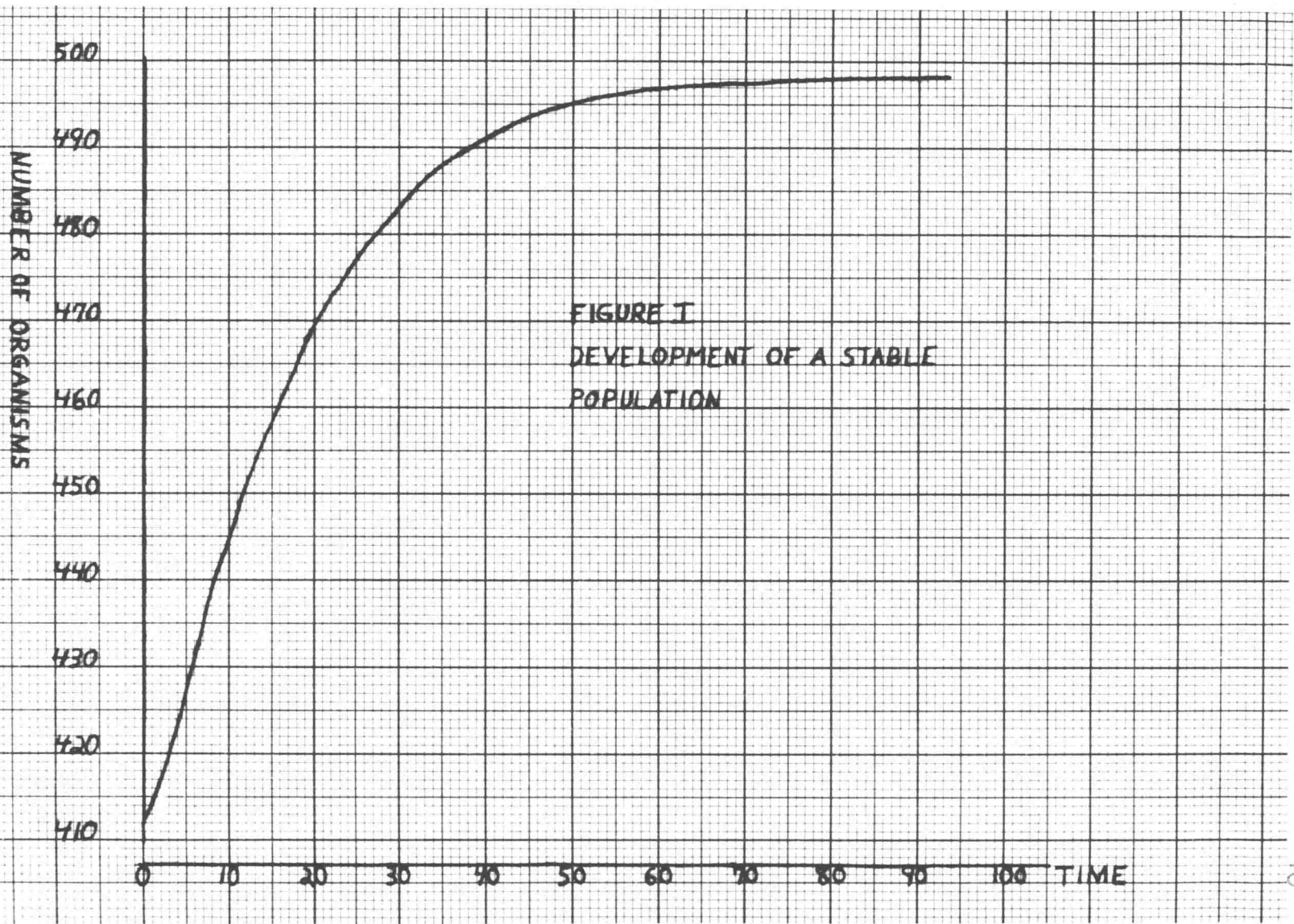
In some fields, especially fisheries, instantaneous mortality rates are important. As an example, let us assume that a fish population has a natural mortality rate of 25 per cent and a fishing mortality rate of 30 per cent. At the end of a year the total mortality rate would not be 55 per cent of the population at the beginning of the year. The population size would be gradually lowered by natural deaths and fishing during the year. Therefore the 30 per cent fishing mortality would be acting on a different size population at one time than at another time.

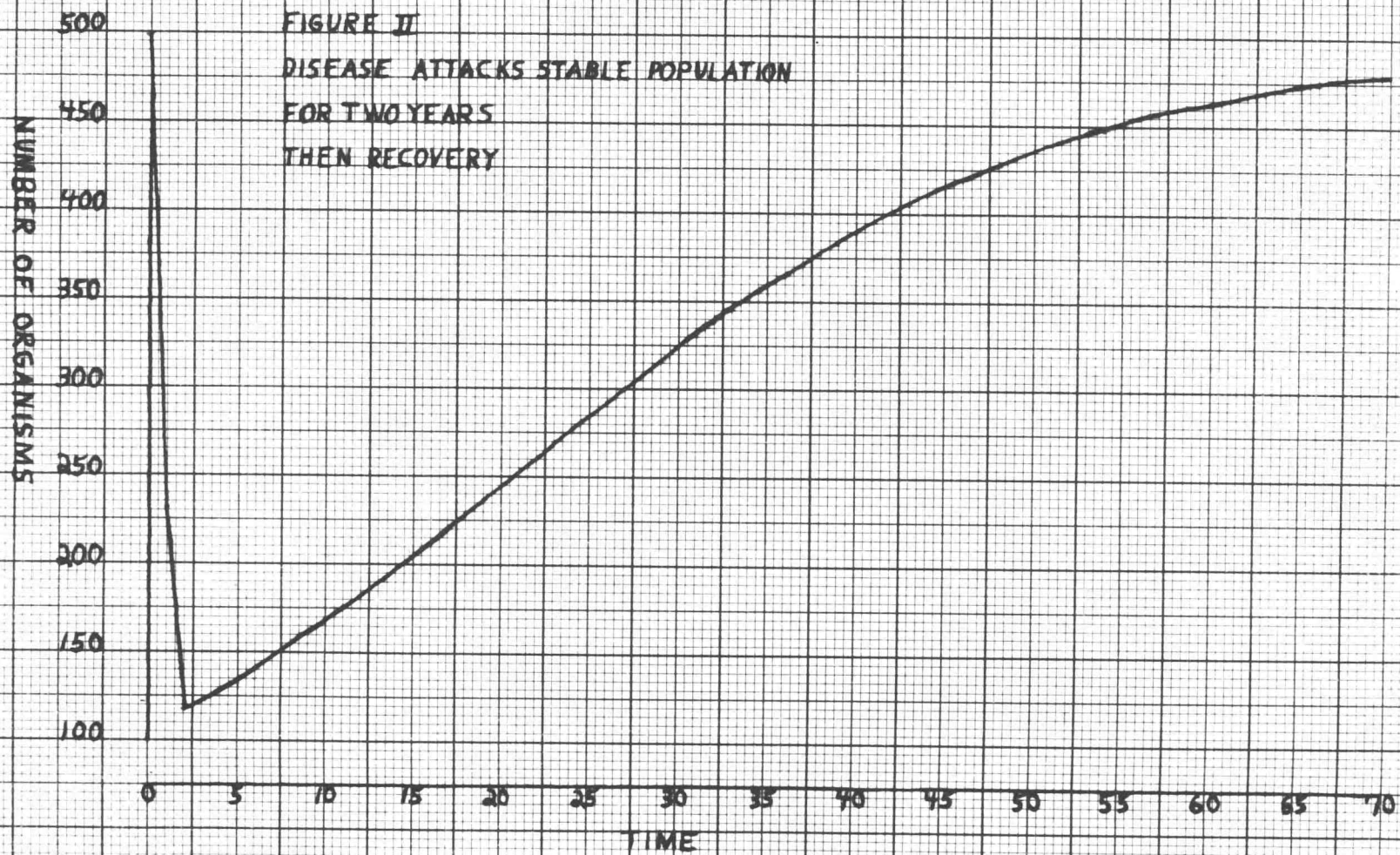
To handle this type of situation the time intervals would have to be shortened. Since this is a discrete model, only close approximations could be made. The time interval could be taken as a week or a month instead of a year. Here, if the population reproduced annually, the N_0 class would be added only every 52 or 12 cycles. Taking the time interval as a day would present difficulties, since the program must go through 365 cycles to cover one year. This could be prohibitive because of the time involved.

If a population has a high birth rate with a large infant mortality, the first year could be better handled if it were divided into smaller time intervals, say monthly intervals. Thus the N_0 class would go through

12 cycles to become the N_1 class. After these cycles the rest of the population would go through one cycle and a new N_0 class would be formed. Without the above consideration, it would be very difficult to find a satisfactory value for f_0 . This is true because first-year mortalities are likely to occur at a shifting instantaneous rate.

If the size of the different age classes in a population are known, or can be estimated over a period of years, this program can be modified to give estimates of other factors. In other words, if everything but d is known or estimated in the equation $N_i = N_{i-1} [f_{i-1} + c \sum N + d \sum M]$ can be solved for d . By repeating this procedure over several years and age classes, estimates may be made of compensatory mortality, predation pressure, and other factors.





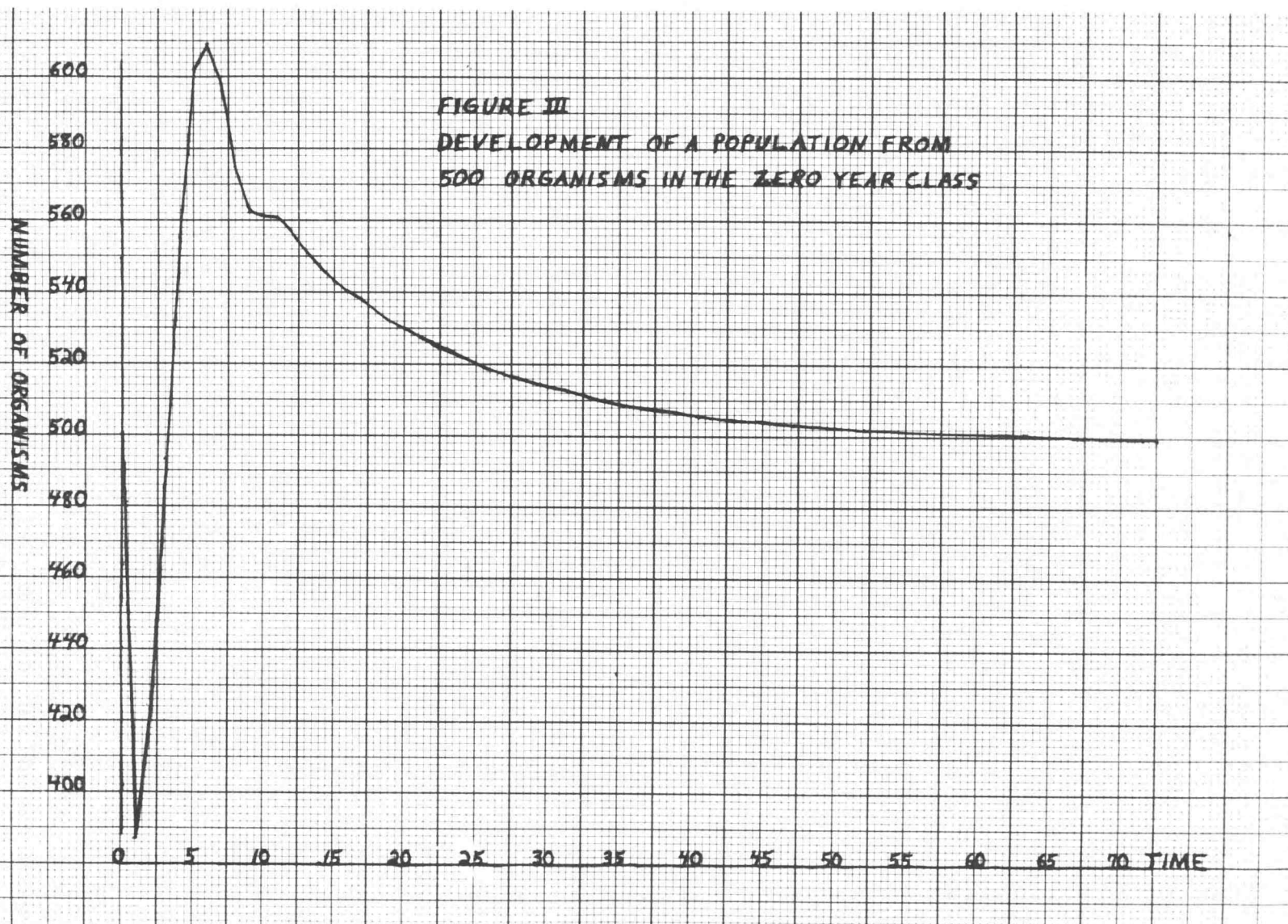
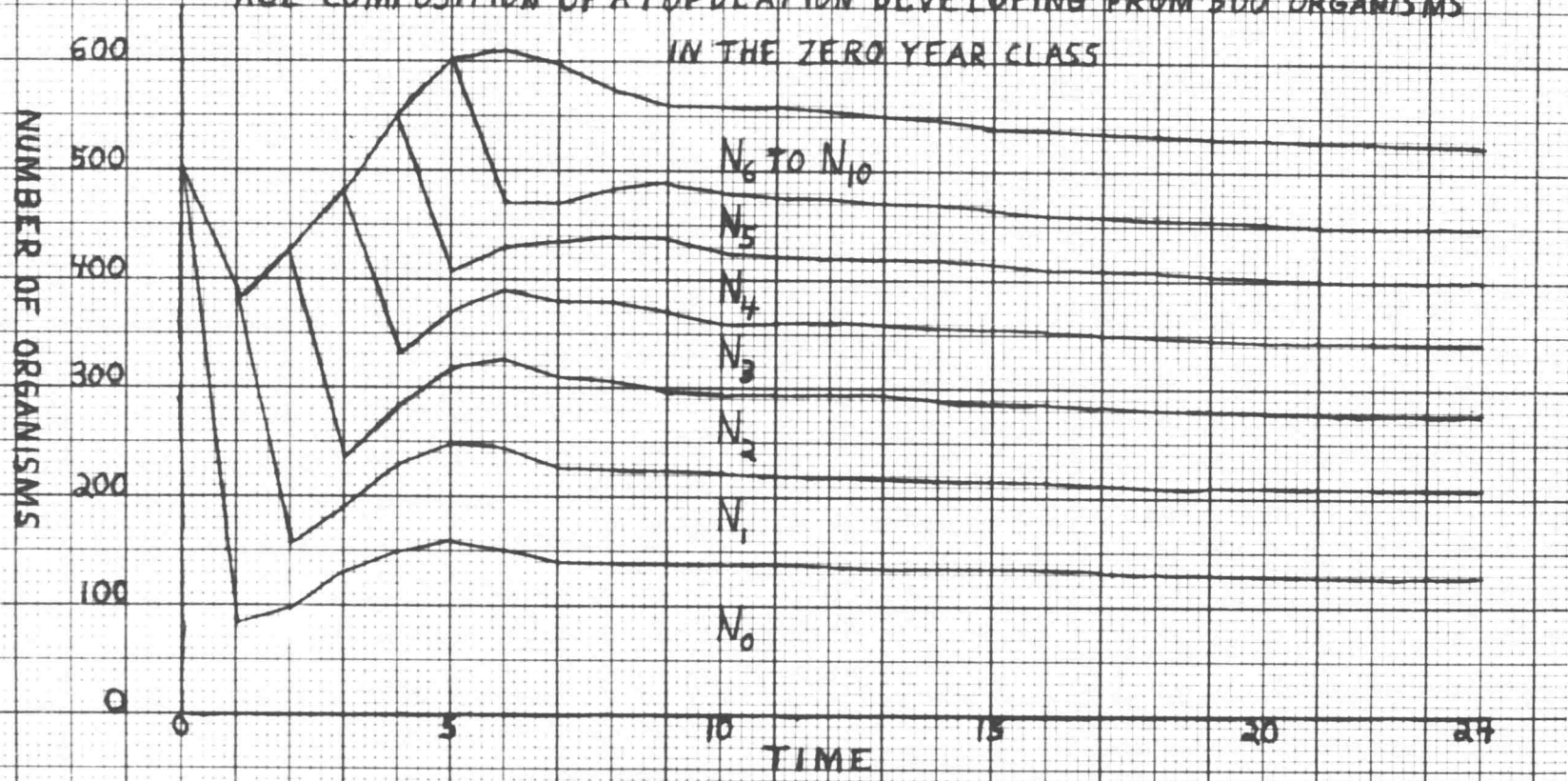
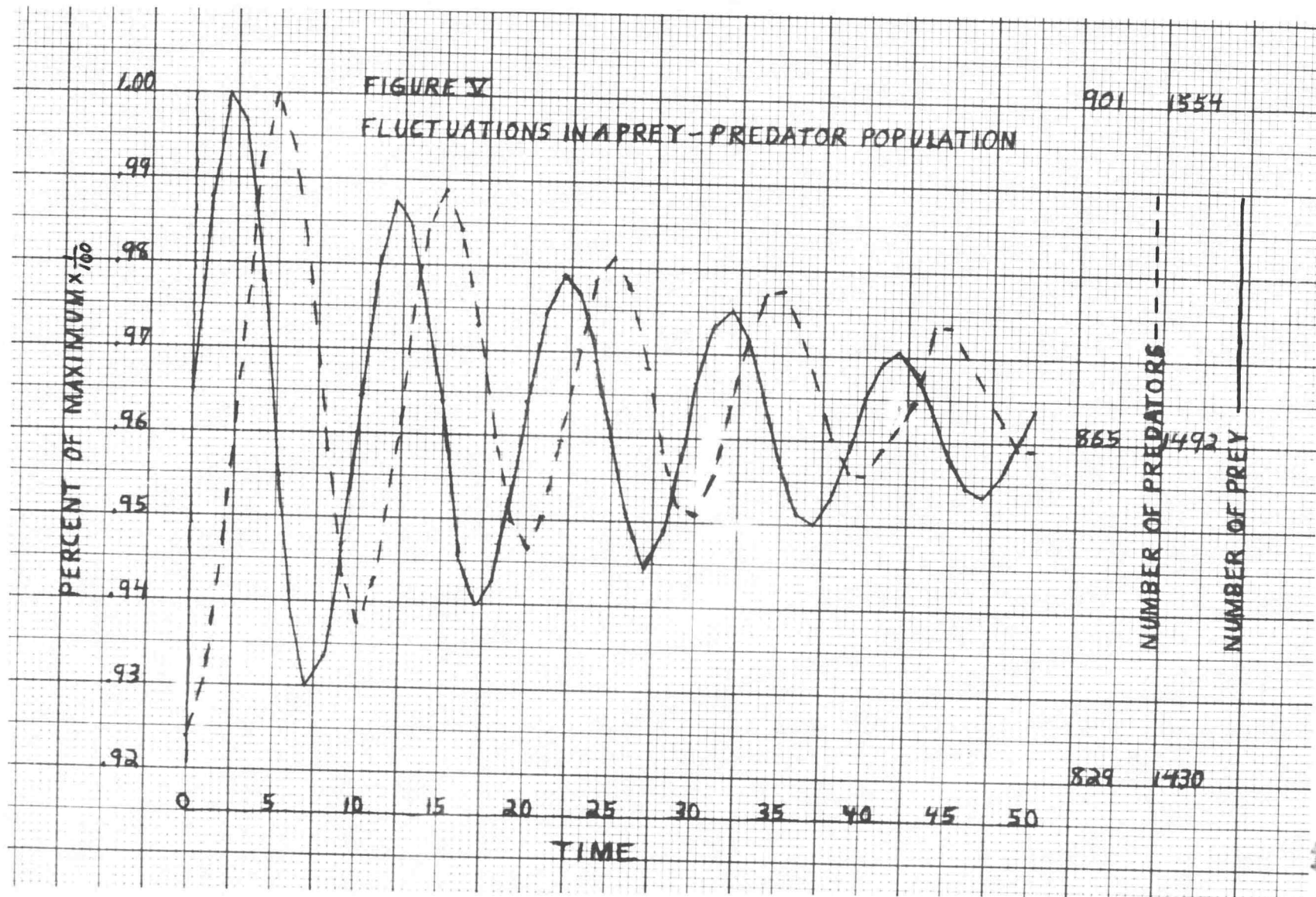


FIGURE IV

AGE COMPOSITION OF A POPULATION DEVELOPING FROM 500 ORGANISMS
IN THE ZERO YEAR CLASS





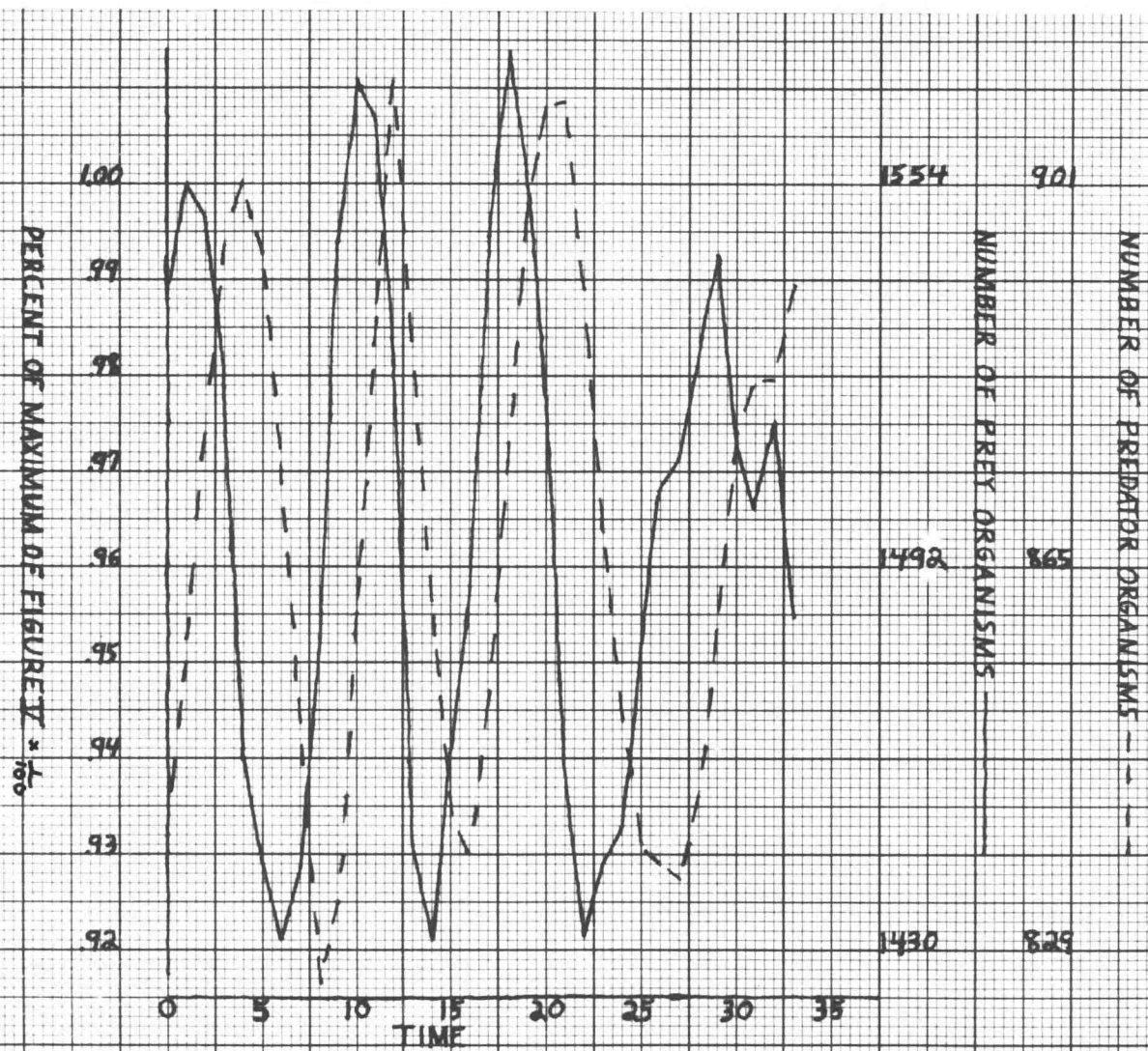
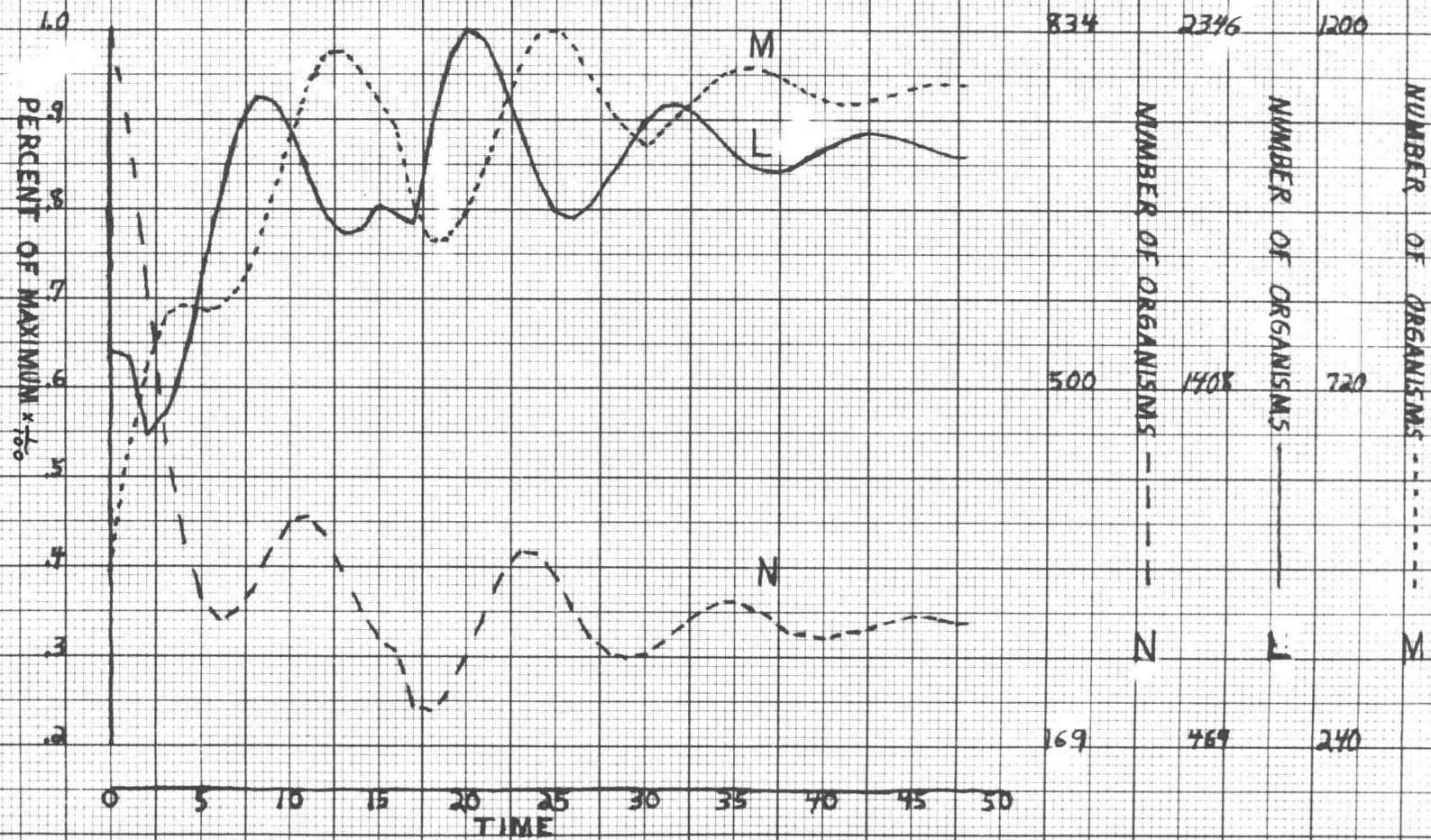
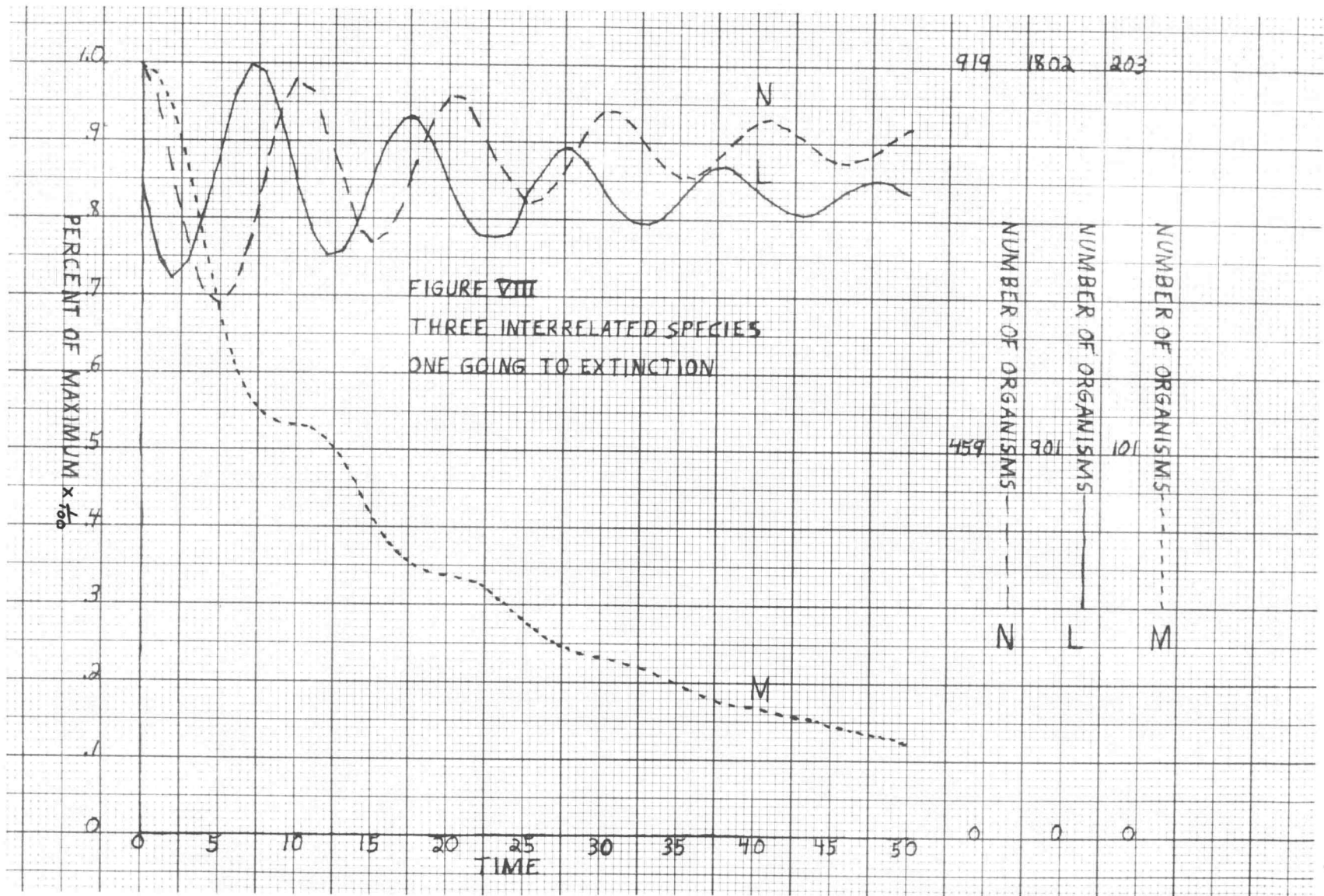


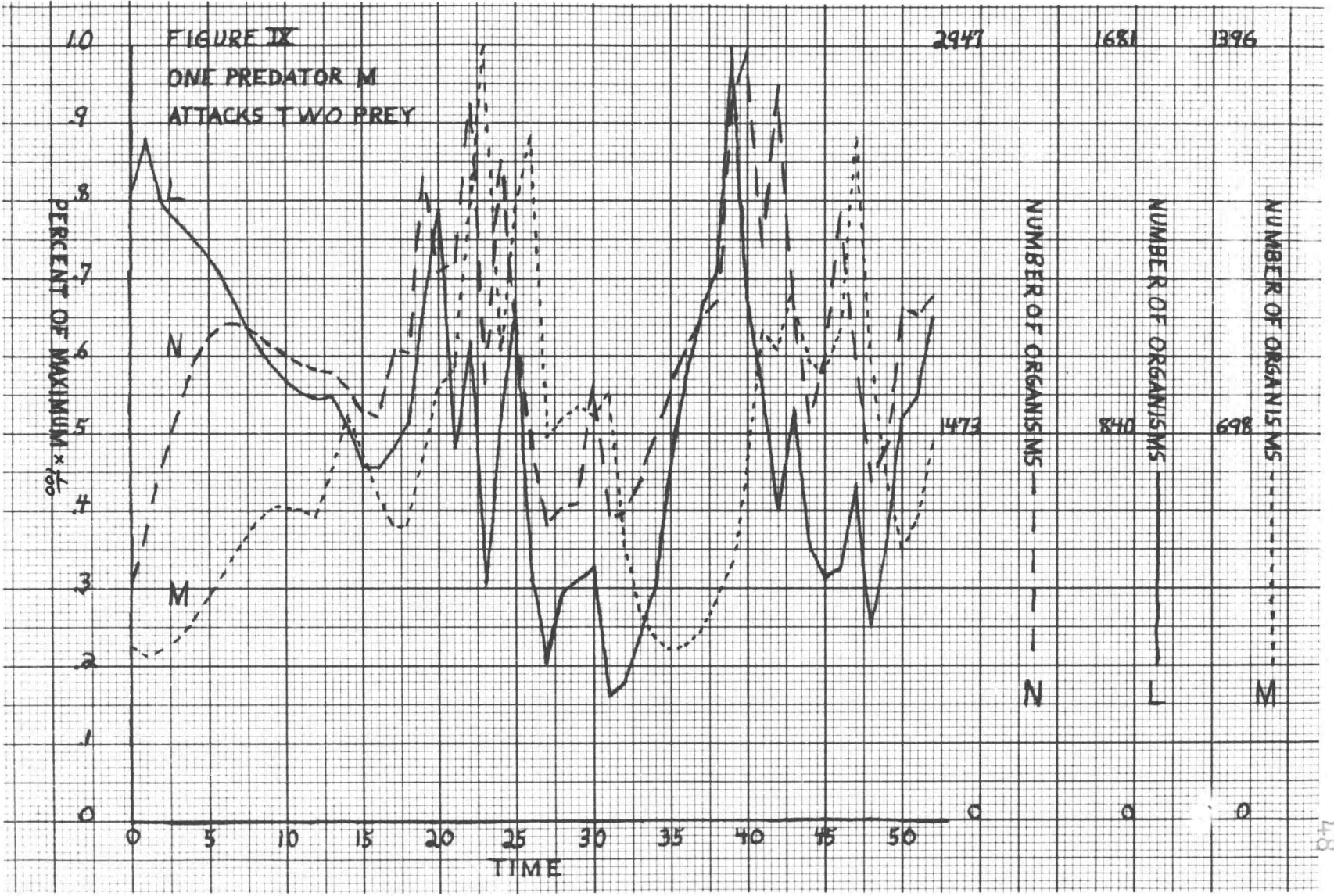
FIGURE VI
PREY-PREDATOR
OSCILLATIONS
WITH CLIMATE
AS A RANDOM
VARIABLE

FIGURE VII

THREE INTERRELATED SPECIES







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