

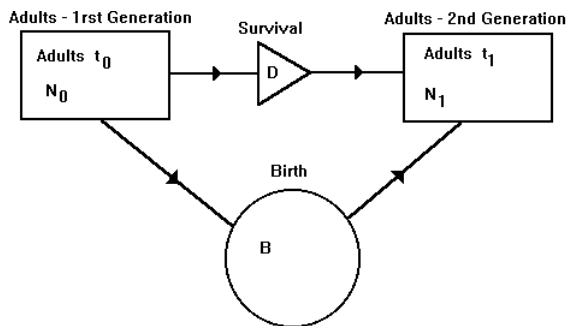
Population growth and regulation:

This material corresponds to Chapter 14 in Ricklefs, but since I use a different mathematical notation, it is presented here independently. You should skim all of Chapter 14 in Ricklefs; specific references to that material will be noted.

Reproduction in organisms can be **modeled**. Modeling analyzes the basic biology of the situation, translates this into numbers and equations, and attempts to validate the model by showing its predictive ability in the “real world” or in controlled experiments. We will start with the simplest model for population growth, the **exponential model**.

Understanding exponential growth models

Our model for exponential growth is for a very specific type of population. The population is **closed** - that is there is no **emigration** or **immigration**. In addition, it is assumed that young produced by one generation will be reproducing adults by the next breeding season. To help understand how the model is derived, let us examine the following life-table diagram:



In this diagram, the initial population of adults is designated N_0 . Time is represented by t , so t_0 means generation 1, t_1 means generation 2, and $t+1$ means the next generation in a sequence. Deaths of adults from one generation to the next are denoted by D , which is a number between 0 and 1. For instance, if 25 out of every 100 adults dies from one generation to the next then $D = 0.25$. The number of births per individual is designated by B , and may be any number 0 or greater. For instance, if an asexually reproducing population of female aphids produces, on average, 16 young per aphid, then B would be 16. Remember that in a population of sexual organisms, you must 'average' the births over both males and females, so, if our aphid population also contained males you would have to divide the total number of births by the total number of aphids, both male and female, to obtain the average number of births per individual (B). Thus a population of

Figure 3: Model of life processes

20 females and 10 males producing a total of 320 young would yield a B of 10.666. Note that B is a measure not only of birth, but also survival to become an adult of the next generation.

To calculate the size of N_1 given N_0 , B , and D is a simple matter. First calculate the number of births:

$$N_0 B$$

Equation 1

Next calculate the survivors:

$$N_0(1 - D)$$

Equation 2

Note that to get the number of survivors, you must subtract the percent dying from 1. Finally, add the births and survivors together. In practice, it is easier to do it all in one step:

$$N_1 = BN_0 + (1 - D)N_0$$

Equation 3



Now for a little algebra. Note that both the births and deaths are multiplied by the size of the former generation. We can factor that out to obtain:

$$N_1 = N_0(B+1- D)$$

Equation 4

To simplify things, define $R = (B + 1 - D)$. The new term, R , can be called the rate of increase (or decrease, if $D > B+1$). Now,

$$N_1 = N_0R$$

Equation 5

If we assume that conditions do not change (a risky assumption) then B , D , and thus R will be the same from generation to generation. Thus:

$$N_2 = N_1R,$$

but since $N_1 = N_0R$ we can say:

$$N_2 = N_0RR \quad \text{or} \quad N_2 = N_0R^2$$

Equation 6

Further, we can generalize to future generations as such - the size of a future generation - generation x - will be the size of the first generation times R raised to the x power, or:

$$N_x = N_0R^x$$

Equation 7

For a concrete example, let's assume a B of 5, a death rate of 35%, and an initial population of 75. The size of the tenth generation would be:

$$R = (1 + 5 - 0.35) = 5.65 \quad \text{and}$$

$$N_5 = 75 * 5.65^{10} = 75 * 33,150,072 = 2,486,255,413$$

Exponential growth takes on a characteristic shape if it is placed on a graph. With normal axes, the shape is that of the letter 'J'; with the y-axis on a logarithmic scale, the population growth lies on a straight line.

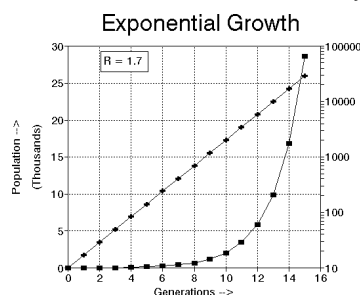


Figure 4 -Graph of exponential growth

started from more than 10 individuals).

In this graph, the straight line represents the data plotted on the log scale to the right, and the curved line represents the data plotted on the normal scale to the left. The initial population size was 10 and R was equal to 1.7. Since one person's 'J' is different from the next, it is actually the straight-line plot on the log scale that is used as "proof" of exponential growth. Note that after only 15 generations, the population size is in the hundreds of thousands, and almost doubling each generation. If this population was bacteria in your chicken salad with a generation time of about 30 minutes on a warm day, you would certainly notice them (particularly if they had



Understanding population growth with age classes

Populations are often more complex than those described by the simple exponential growth model. In particular, one of the assumptions, that the newborn organisms are reproductively mature by the next breeding season, is often not valid. Many populations can be divided into **age classes**. For instance, there can be newborns, juveniles, young adults and old adults. This population would be said to have four age classes. Further, it is not unreasonable to assume that each of these groups will have different fertility (birth) rates, and different probabilities of survival.

In the drawing to the right, the four age classes are represented by $n_0, n_1, n_2,$ and n_3 . The sum of all four age classes represents the total population size, N . The probability of a newborn surviving to reach the second age class is P_0 , the probability of the second age class reaching the third is P_1 , and so on. By definition, the number of the last age class surviving is 0, thus, in the figure, P_3 is equal to 0. The birth rate of the newborns is F_0 , the birth rate of the second age class is F_1 , and so on. Once again, the population is **closed** - there is no **emigration** or **immigration**.

As you can see, this model is much more complicated than the model for simple exponential growth. Still, the underlying mathematics are very similar. The only difference is that the age classes introduce multiple birth and death rates. Looking at the figure, trace how each generation is formed. The newborns (n_0) of a new generation are the sum of the births to each age class of the previous generation:

$$n_{0,t+1} = n_{0,t} F_0 + n_{1,t} F_1 + n_{2,t} F_2 + n_{3,t} F_3$$

Equation 8

The other age classes of the $t+1$ generation are simply the number of the next younger age class that survive:

$$n_{1,t+1} = n_{0,t} P_0 \quad n_{2,t+1} = n_{1,t} P_1 \quad n_{3,t+1} = n_{2,t} P_2$$

Equation 9

The total population size of the next generation is the sum of the age classes we have just calculated:

$$N_{t+1} = n_{0,t+1} + n_{1,t+1} + n_{2,t+1} + n_{3,t+1}$$

Equation 10

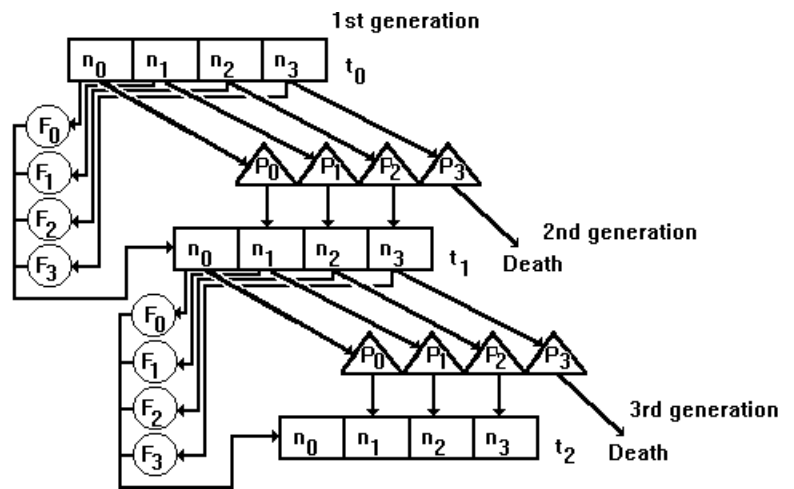


Figure 5: Model of life processes for a population with 4 age classes



For a concrete example, let us assume a population with 5 age classes and the following parameters:

Age Class	n_t	F	P
0 (first)	25	0.5	0.8
1 (second)	20	2.0	0.8
2 (third)	20	2.5	0.7
3 (fourth)	15	2.0	0.4
4 (fifth)	10	1.0	0.0

Looking at the parameters, we can make a few generalizations. First, fertility peaks with the third age class. Presumably, younger individuals are too small, inexperienced, or immature to reproduce as effectively, and older individuals are in less than optimal physiological condition. Survival is fairly constant at first, but drops off

rapidly in the older age classes. The total population size at time $t=0$ is 90.

The number of newborns in the $t+1$ generation will be:

$$n_{0,t+1} = (25 \cdot 0.5) + (20 \cdot 2.0) + (20 \cdot 2.5) + (15 \cdot 2.0) + (10 \cdot 1.0) = 142.5$$

The number of individuals in the remaining age classes is:

$$n_{1,t+1} = (25 \cdot 0.8) = 20 \qquad n_{2,t+1} = (20 \cdot 0.8) = 16$$

$$n_{3,t+1} = (20 \cdot 0.7) = 14 \qquad n_{4,t+1} = (15 \cdot 0.4) = 6$$

$$n_{5,t+1} = (10 \cdot 0.0) = 0 \text{ (there is no sixth age class)}$$

The total population size at time $t+1$ is thus:

$$N_{t+1} = 142.5 + 20 + 16 + 14 + 6 = 198.5$$

We can define R as the **rate of growth** for the population. Between time t and time $t+1$ in this example, R is $198.5/90 = 2.20$. If it were not for the effect of the age classes, this R would be the same as the R in the exponential growth model. When age classes are introduced into the exponential growth model, it is no longer easy to specify what the population will be at some generation in the future. Remember, the exponential growth equation:

$$N_x = N_0 R^x \quad \text{where } R = 1 + B - D$$

allowed us to calculate future population sizes easily. With age classes, all the intervening generations have to be calculated - admittedly a trivial problem with the advent of computers.

A situation does arise, however, where the R calculated from the rate of growth of a population with age classes does not change from generation to generation, and thus can be used to make an estimate of the population size at some arbitrary generation in the future. The value of R stabilizes when the proportion of the total population size represented by each age class no longer changes. This point is known as the **stable age distribution**. In our example above, at time t , the newborns represented $25/90$ or 27.7% of the population, but at time $t+1$ they represented $142.5/198.5$ or 71.7% of the population. If you run this example on the computer using the *EcoCyb* program, you will get the following results (intermediate generations not listed to save space):



Program AgeClass - Calculates Population Size for 1-20 Age Classes

Population Parameters:

F0 = 0.5000 P0 = 0.8000
 F1 = 2.0000 P1 = 0.8000
 F2 = 2.5000 P2 = 0.7000
 F3 = 2.0000 P3 = 0.4000
 F4 = 1.0000 P4 = 0.0000

Generation: 0

N0 = 25.0000 %N0 = 0.2778
 N1 = 20.0000 %N1 = 0.2222
 N2 = 20.0000 %N2 = 0.2222
 N3 = 15.0000 %N3 = 0.1667
 N4 = 10.0000 %N4 = 0.1111
 Total Population Size = 90.0000

Generation: 1

N0 = 142.5000 %N0 = 0.7179
 N1 = 20.0000 %N1 = 0.1008
 N2 = 16.0000 %N2 = 0.0806
 N3 = 14.0000 %N3 = 0.0705
 N4 = 6.0000 %N4 = 0.0302
 Total Population Size = 198.5000
 Rate of Growth = 2.2056

Generation: 2

N0 = 185.2500 %N0 = 0.5579
 N1 = 114.0000 %N1 = 0.3433
 N2 = 16.0000 %N2 = 0.0482
 N3 = 11.2000 %N3 = 0.0337
 N4 = 5.6000 %N4 = 0.0169
 Total Population Size = 332.0500
 Rate of Growth = 1.6728

Generation: 18

N0 = 6574606.4626 %N0 = 0.5988
 N1 = 2748117.0247 %N1 = 0.2503
 N2 = 1148684.2530 %N2 = 0.1046
 N3 = 420120.7802 %N3 = 0.0383
 N4 = 87803.0753 %N4 = 0.0080
 Total Population Size = 10979331.5960
 Rate of Growth = 1.9139

Generation: 19

N0 = 12583292.5490 %N0 = 0.5988
 N1 = 5259685.1701 %N1 = 0.2503
 N2 = 2198493.6197 %N2 = 0.1046
 N3 = 804078.9771 %N3 = 0.0383
 N4 = 168048.3121 %N4 = 0.0080
 Total Population Size = 21013598.6280
 Rate of Growth = 1.9139

Generation: 20

N0 = 24083456.9300 %N0 = 0.5988
 N1 = 10066634.0390 %N1 = 0.2503
 N2 = 4207748.1361 %N2 = 0.1046
 N3 = 1538945.5338 %N3 = 0.0383
 N4 = 321631.5908 %N4 = 0.0080
 Total Population Size = 40,218,416.230
 Rate of Growth = 1.9139

Note that the rate of growth (R) and the percent of the total that each age group comprises are no longer changing by generation 20 (actually, stabilization occurred earlier). Once the stable age distribution is achieved, overall population size can be determined simply by multiplying the previous generation population by R , and the size of any age class by multiplying by the appropriate percentage.

Now, you might ask, what happens if we try to substitute the exponential equation to determine population size at generation 20:

$$N_{20} = N_0 R^{20} = 90 * 1.9139^{20} = 39,140,589.13$$

The computer calculated 40,218,416.23 by iteration, a difference of 1,077,827.105; this is not a bad range of error for ecology.

The ability to substitute the exponential equation for iterative calculation would be worthless if there was no way to calculate the stable age distribution without iteration! In other words, the stable age distribution and the value of R we just used were calculated by iteration from generation to generation. If we then use these values to estimate population size we're really being pretty stupid, since we could just let the computer give us an 'exact' solution for the generation we are interested in. Fortunately, there is a way to calculate the stable age distribution



without doing the iterations. To do this we set up and solve the **stable age distribution polynomial**. We won't go into the details, primarily because computers have made it obsolete. In the time before computers, though, this method saved a lot of work.

The main point of the stable age distribution and R from our standpoint today is that it shows that a population with age classes eventually grows in a way that closely resembles what a simple population would do using our formula for exponential growth. Is our model of population growth with age classes an example of exponential growth? Remember our criteria - a straight line on a log plot. If we graph the data from our example, we get a graph that looks like this:

Note that there are some fluctuations in the age class sizes; then they, as well as the overall population size, settle down into exponential growth. As proof, the log plot of the overall population size becomes a straight line by generation 3! Once the stable age distribution has been reached, growth is clearly exponential not only for the population as a whole, but for the age classes as well. In some graphs, depending on the initial parameters, the lines may cross on their way to the stable age distribution. In the final distribution, the position of the lines is determined by the F 's and P 's. In a population such as ours, with relatively high birthrates and progressively lower survival, there are of course more individuals in the youngest age class and progressively fewer in the older classes.

In summary, the addition of age classes to an exponential population growth model does not change the overall characteristics of growth, only some of the details. By the time a stable age distribution is reached (often in only a few generations) growth of the population is indistinguishable from normal exponential growth. Models with age classes are often more realistic than those without, and are an important tool in such areas as wildlife management. Calculation of the stable age distribution by solving the stable age polynomial, an important procedure in pre-computer days, is less useful today.

Biology of exponential growth models:

Exponential growth is sometimes called density independent growth because the biological factors which limit growth in these case are not affected by population size. The classic example of exponential population growth is found in insect populations which continue to increase throughout the summer, only to die off with fall frosts. Obviously, most populations do not continue to grow exponentially. Things that control population growth will be introduced later.

The life table:

Life tables are important in describing the demographics of a population, that is, how many individuals there are, how old they are, and how long they can expect to live. The example in Table 14.4 in Ricklefs is useful. The first column has the age, x . In this case, x is measured in 3-month intervals so an individual in the bottom row would be 24 months or 2 years old. The number alive is a simple numerical count of the number fitting into each of the age classes in the previous column. It is used for all subsequent calculations. Survivorship (l_x) is calculated by multiplying out the probability of survival in each of the previous age classes. Mortality rate (m_x) is determined by subtracting the number alive in one age class from the number alive in the previous age class, then dividing that number by the number in the previous age class. For example, in the first line mortality is equal to $843 - 722 = 121$; $121/843 = 0.143$. Survival rate (s_x) is calculated by dividing the number alive in that age class by the number alive in the previous age class. The expectation of life is also determined mathematically; we needn't go into the details. Fecundity is measured by counting the number of offspring per female in each of the age classes.

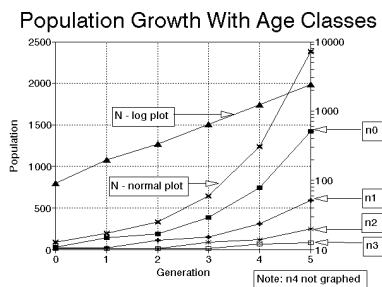


Figure 6: Graph of Exponential Growth in a Population With Age Classes.



Estimates of survival in natural populations:

The life table we just discussed is a dynamic life table, where the data is gathered from a population of organisms over the lifespan of at least one set of organisms. If you don't have the time to do this (it can take a couple of millennia for some trees), you can estimate the values by determining how old the organisms are when they die and thus produce a static life table (Table 14.5 in Ricklefs).

Logistic growth - overview:

So far, our models of population growth have been based on exponential growth - a population begins to grow and continues to increase logarithmically over time, with no end in sight. Because the size of the population does not affect the growth rate, such growth is often referred to as **density independent growth**.

While some populations no doubt increase exponentially, at least for a time (rabbits in Australia, bacteria in potato salad at a picnic ...) it is apparent that such growth cannot go on indefinitely. Thus, while exponential growth models may be useful under some conditions, as a model of real-life population growth they often fail.

To address the inadequacies of the density *independent* exponential growth model, a new model can be derived. This model will be sensitive to the size of the population, thus it will be a **density dependent** model. For historical reasons, it is often called the **logistic** model (logistic has to do with supplies like food, not logarithms).

Before the mathematics, let's examine the biological assumptions underlying the logistic model. First, it assumes that an increase in population size will lead to a decrease in birth rate, presumably because more potential mothers will be competing for a limited set of resources (food, nest sites, etc.). Not only might the individual mothers not be able to obtain enough resources to produce a large litter, but the time and energy they expend competing for resources will also lower the birth rate. On the other side of the ledger, it is expected that at high densities, death rates will increase. This probably occurs because starvation, fighting, disease, parasites, etc. are more prevalent under crowded conditions.

Derivation of the model:

Now for the formula. First, our birth rates. If we assume the density **independent** birth rate to be similar to the birth rate in our exponential growth model, we can call it B . We'll actually call it B_0 because it represents the original birth rate (when the population is small). Now, let's assume that each additional individual in the population reduces the birth rate slightly. We'll call this reduction b , the density dependent birth rate, and to find its effect on the overall birth rate we will multiply it by the overall population size, N , and subtract the result from the density independent birth rate:

$$\text{Overall birth rate} = B_0 - bN$$

Equation 11

Similar reasoning can be applied to the death rates. If the density independent death rate is D_0 , then the effect of additional individuals can be called d , and the death rate can be represented by:

$$\text{Overall death rate} = D_0 + dN$$

Equation 12

These two equations allow us to create an equation to represent population growth:

$$N_{t+1} = (B_0 - bN_t)N_t + [1 - (D_0 + dN_t)]N_t$$

Equation 13



This is the equation for logistic growth. It consists of the birth rate, $B_0 - bN_t$, times the population size of generation t , plus the number of survivors, $1 - (D_0 + dn_t)N_t$. Note that if there is no density dependence, b and d are equal to zero and you have the exponential growth equation again:

$$\begin{aligned} N_{t+1} &= (B_0 - bN_t)N_t + [1 - (D_0 + dn_t)]N_t \\ &= (B_0 - 0N_t)N_t + [1 - (D_0 + 0n_t)]N_t \\ &= B_0N_t + (1 - D_0)N_t \end{aligned}$$

Equation 14

Compare Equation 3 on page 1 to the third line of Equation 14

The logistic model - an example:

This simple model has some amazing properties, which we will examine in some detail. First, let's run an example through the computer and plot the results.

Assume a population of bass in a pond. When the first bass are put in, there is an abundance of food (bluegills), and few constraints on population growth. Suppose that the birth rate measured at this point is 1.3, that is, for every fish in the population 1.3 young are born (and survive to adulthood) every year (if the sex ratio is 1:1 this means that each female has 2.6 young that actually survive). At this stage, we will ignore the effects of age classes by defining birth as survival to adulthood. Let's place a death rate of 20% (these are primarily the young bass getting eaten). Let us further assume that each additional bass in the pond decreases the birth rate 1/2% (by eating bluegills) and increases the death rate by 1/2% (by eating young bass and increasing the risk of starvation, parasites and disease). Initially, the pond is stocked with 2 bass. Putting these values into our equation we get:

$$N_{t+1} = (1.3 - (0.005 \cdot 2)2) + [1 - (0.2 + 0.005 \cdot 2)]2$$

$$N_{t+1} = 2.58 + 1.58 = 4.16$$

In the next generation:

$$N_{t+2} = (1.3 - (0.005 \cdot 4.16)4.16) + [1 - (0.2 + 0.005 \cdot 4.16)]4.16$$

$$N_{t+2} = 5.32 + 3.24 = 8.56$$

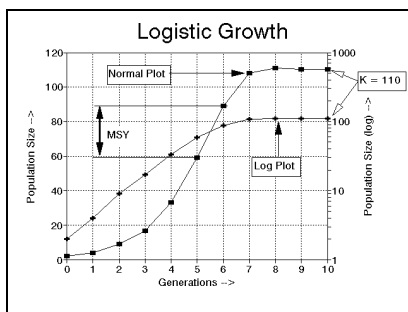


Figure 7: Graph of logistic growth

If we graph the data for ten generations, we get the graph to the left. Note the 'S' shape of the curve; typical of the logistic growth model. The log plot shows an initial burst of nearly **exponential growth**, followed by a decline as the population size increases and the density dependent factors begin to reduce the rate of population increase. The maximum increase in population from one generation to the next occurs at the middle of the curve at generation 5 and is an important management tool known as the **maximum sustainable yield (MSY)**; for this pond it is equal to 30. In theory, it is possible to remove (by fishing) 30 bass each year if the population is not allowed to fall below 59 bass. At this point, the population is almost doubling each year. Below this point, the population is doubling, but there aren't as many fish to double, and above this point, density dependence means that the birth rate drops and the population no longer doubles. The population levels off at about 110, this is the **carrying capacity** of the pond, and is designated **K**.



The value of K can easily be calculated from the initial parameters:

$$K = \frac{(B_0 - D_0)}{(b + d)}$$

Equation 15

In our example:

$$K = \frac{(1.3 - 0.2)}{(0.005 + 0.005)} = \frac{1.1}{0.01} = 110$$

If the population exceeds the carrying capacity, then the next generation will see a decrease in population. If the population is less than K , the population will increase the next generation.

Two additional terms can be derived. The **intrinsic rate of increase** is called r , and is the difference between the density independent birth and death rates:

$$r = B_0 - D_0$$

Equation 16

In our example:

$$r = 1.3 - 0.2 = 1.1$$

We can also define another growth rate R_0 , which is the same as the R in the exponential growth equation. This R_0 tells us a lot about how the model will behave, and is formulated as follows:

$$R_0 = 1 + (B_0 - D_0)$$

Equation 17

In our bass example,

$$R_0 = 1 + (1.3 - 0.2) = 2.1$$

R_0 and chaos:

Here comes the critical part for R_0 : if R_0 is less than 1, the population cannot grow, and becomes extinct (K is negative). If R_0 is greater than 1 but less than 2, the population will approach K smoothly. If R_0 is between 2 and 3, (as in our example), the population will approach K , but will oscillate above and below K for a while; these oscillations will decrease in size, however. If R_0 is between 3 and 4, the oscillations will not decrease in size. This is a very interesting result, because a population in this condition exhibits **chaotic** behavior. This is an example of a very simple model producing a very complex behavior, because the chaotic fluctuations appear random, but are not. Other examples of chaotic systems are weather patterns and some predator-prey models (based on the logistic equation). Above 4, R_0 values indicate oscillations in population size that continue to increase in size, eventually leading to extinction.



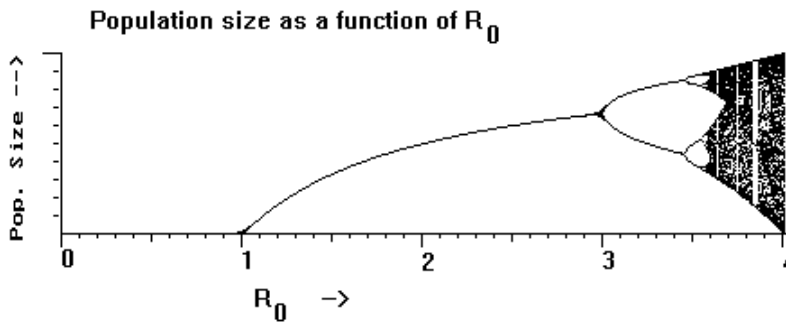


Figure 8 Graph of population size showing chaotic behavior

The figure to the left shows a plot of R_0 versus population size (population size is abstracted here as a number between 0 and 1). From $R_0 = 0$ to $R_0 = 1$, the population size is zero. From $R_0 = 1$ to $R_0 = 3$, there is a single value for the population size. From $R_0 = 3$ to $R_0 = 4$ we get first two, then four, then more oscillations until there is no apparent correlation between R_0 and the population size. Above $R_0 = 4$ some of the

oscillations are so large that the population reaches 0 -- extinction.

Perhaps even more interesting, as the graphs below show, is that there is much apparent order in this apparently random set of fluctuating population sizes. The next two graphs are enlargements of section of the graph above them, revealing increased detail. Note that a region of many possible population values suddenly gives rise to a region with maybe four possible values, which in turn goes back to a region with hundreds of possibilities. If you keep on magnifying a region, this pattern of alternating regions is repeated over and over. The computer program CHAOS (part of the ECOCYB program) will demonstrate this if you are interested.

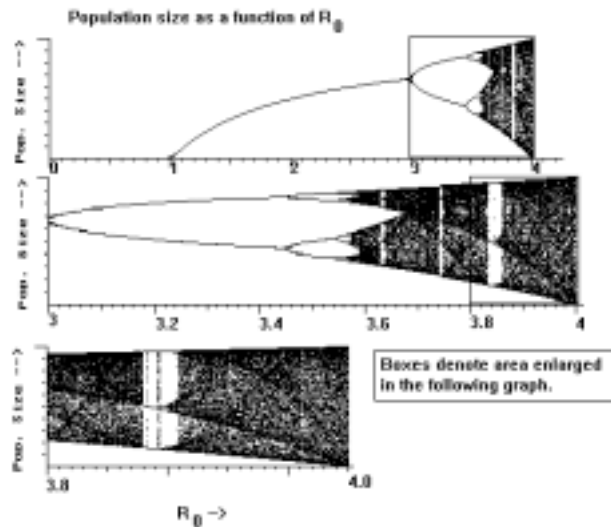


Figure 9: Graphs showing detail of chaotic regions

The chaotic nature of the logistic equation has been an area of much recent interest. You might want to read *Chaos: Making a New Science* by James Gleick, or even the novel *Jurassic Park* by Michael Crichton for more information. The book has a much better discussion of the phenomenon; in the movie this rather simple technical material was turned into a muddled scene where Jeff Goldblum tries to get into Laura Dern's pants.

Other forms of the logistic equation:

Finally, there are other ways to write the logistic equation. With K and r defined as follows:

$$K = (B_0 - D_0)/(b + d)$$

$$r = B_0 - D_0$$

we can rewrite the logistic equation as follows:

$$N_{t+1} = [1 + r - (r/K)N_t]N_t$$

Equation 18



Alternately, we can look at the change in population size and rewrite the logistic equation as follows:

$$\Delta N = rN(K - N)/K \quad (\text{note: } \Delta \text{ means 'delta' or change})$$

Equation 19

and the population size of generation t+1 would be:

$$N_{t+1} = N_t + rN_t(K - N_t)/K$$

Equation 20

In summary, the logistic model is a simple modification of the exponential growth model, with factors added to decrease birth rates and increase death rates as the population size increases. This makes for a more realistic model in which populations control their own growth to some extent. The logistic model results in a typical 'S' shaped normal plot of population growth, with the log plot showing an initial straight-line (exponential) growth rate which tapers off. The logistic growth curve also demonstrates the maximum sustainable yield concept important in management programs for living populations. Three parameters can be derived from the logistic model: K , the carrying capacity, indicates what level the population will reach an equilibrium at, r , the intrinsic rate of increase, which determines how fast K will be reached, and R_0 , which determines the stability of K and how the population will approach K . Under conditions where R_0 is greater than 3, the logistic model exhibits chaotic behavior which is apparently random but actually has an underlying order.

Stochastic extinction of small populations:

(page 306 in Ricklefs)

A model is presented here which ties the probability of extinction to the birth rates, death rates, and population size of a population. A simplified version for use when birth rates equal death rates, is presented in the text:

$$p_0(t) = \left[\frac{bt}{1 + bt} \right]^N$$

Equation 21

Consider an example. If $b = 0.5$ and $t = 100$ years, if we start with an initial population (N) of 100 the probability that the population will go extinct in 100 years is:

$$p_0(100) = \left[\frac{0.5 \times 100}{1 + 0.5 \times 100} \right]^{100} = \left[\frac{50}{51} \right]^{100} = 0.984^{100} = 0.1435$$

This answer can be verified in Table 16.1 in Ricklefs. It means that there is a 14% chance that the population will become extinct in the next 100 years (and an 86% chance that it will *survive*). In examining Figure 15.19 in Ricklefs note that large populations face only a slight risk of extinction (except over long periods of time) and that small populations face a considerable risk, even over short periods of time.



Key Equations:

Exponential Growth:

$$N_x = N_0 R^x$$

Exponential Growth with Age Classes:

$$n_{0,t+1} = n_{0,t} F_0 + n_{1,t} F_1 + n_{2,t} F_2 + n_{3,t} F_3$$

$$n_{1,t+1} = n_{0,t} P_0 \quad n_{2,t+1} = n_{1,t} P_1 \quad n_{3,t+1} = n_{2,t} P_2$$

$$N_{t+1} = n_{0,t+1} + n_{1,t+1} + n_{2,t+1} + n_{3,t+1}$$

Logistic Growth

$$N_{t+1} = (B_0 - bN_t)N_t + [1 - (D_0 + dN_t)]N_t$$

K:

$$K = \frac{(B_0 - D_0)}{(b + d)}$$

