

Chapter 2

Exploring Dynamic Biological Systems

Art may be said... to overcome, and advance nature, as in these Mechanicall disciplines.

(Wilkins, Mathematical Magick, 1648)

2.1 Simple Population Dynamics

In this chapter we will return to the concepts and ideas presented above, and explore in more detail the dynamics of seemingly simple dynamic population models. In the process of developing and exploring these models you will learn more about the features of the STELLA software. The findings of this exploration should sensitize your perception of dynamic processes and help you develop your dynamic modeling skills.

Let us begin with a simple model of a population N in a given ecosystem with carrying capacity K . The initial size of the population is $N(t=0)=10$, and the carrying capacity is $K=100=\text{constant}$. For population sizes below the carrying capacity, N will increase. Above the carrying capacity, N will decrease. The maximum rate of increase of N is $R=0.1$, measured in individuals per individual in N per time period. A convenient specification for the change in the population size is the logistic function

$$\Delta N = R * N * \left(1 - \frac{N}{K}\right) \quad (2.1)$$

To set up the STELLA model for our investigation of the dynamics of this population, use the reservoir icon for the stock N , the flow symbol for ΔN , and

A save-disabled version of STELLA and the computer models of this book are available at www.iseesystems.com/modelingdynamicbiologicalsystems.

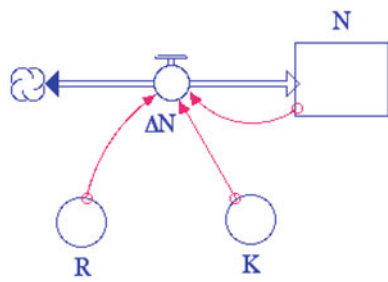


Fig. 2.1

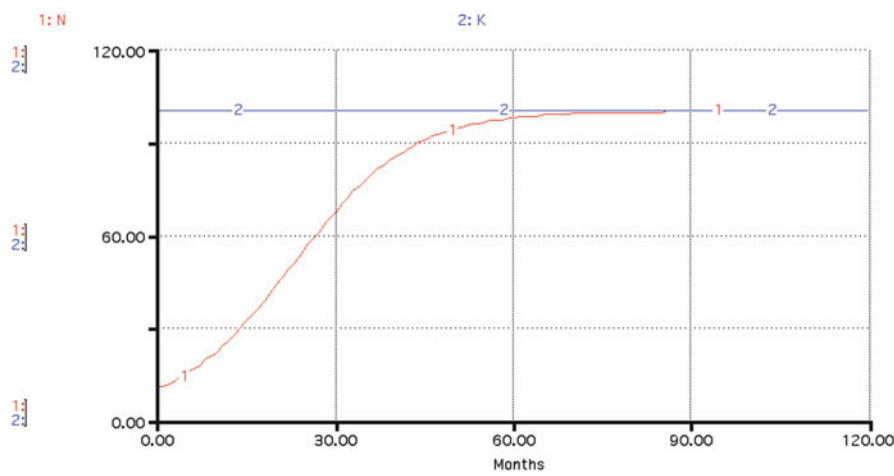


Fig. 2.2

converters for the transforming variables R and K. Specify the flow ΔN as a biflow by clicking on the biflow option in the side-docked panel. Your model should look like the one in Fig. 2.1.

Set up a graph to plot N and K over time. Specify in the Run Specs menu a DT of one and the length of the model run to extent from time period 0–120, and specify the units of time as months. Before you run the model, make an educated guess of the population size N over time. Will N reach the carrying capacity? Will the approach be exponential? Will N overshoot K? Here is what you should get when you run your model (Fig. 2.2).

The population size N asymptotically approaches K, and this approach is at first fairly rapid—as long as N is far below K—but the increase slows down as K is approached. The ratio of N/K approaches 1 as N increases, and thus $(1 - N/K)$ becomes ever smaller. As a result, ΔN approach zero, but it never quite gets there. Experiment with alternative values for R, K and initial population sizes, and observe the resulting population dynamics. Always make an educated guess about the results before you run the model.

2.2 Simple Population Model Equations

$$N(t) = N(t - dt) + (\Delta N) * dt$$

$$\text{INIT } N = 10$$

INFLOWS:

$$\Delta N = R * N * (1 - N/K)$$

$$K = 100$$

$$R = .1$$

2.3 Simple Population Dynamics with Varying Carrying Capacity

Let us now explore the dynamics of this system by making small changes to the parameter values. We have already modeled in the previous chapter the case in which the rate of natural increase changes as a function of the population size. Another parameter that may not be constant over time is the carrying capacity K . For example, there may be seasonal fluctuations in the physical environment that affect the resource base on which our population feeds. For simplicity, we assume that these seasonal fluctuations occur along a sinewave around the carrying capacity of 100. Click on the converter for K , then type “100+” and scroll down in the list of built-in functions to find SINWAVE to add SINWAVE to the value 100. The built-in function SINWAVE requires an amplitude and period for its specification. We set those arbitrarily to 10 and 12, respectively. You should now have

$$K = 100 + \text{SINWAVE}(10, 12) \quad (2.2)$$

which yields a carrying capacity that fluctuates between 90 and 110 over the course of a twelve-month period. The STELLA diagram (Fig. 2.3) should look as before, but the results (Fig. 2.4) are different because of the change in the specification of ΔN .

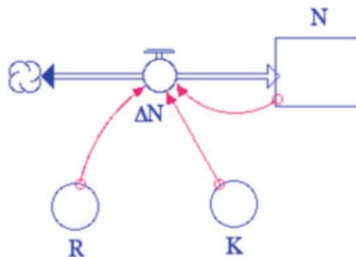


Fig. 2.3

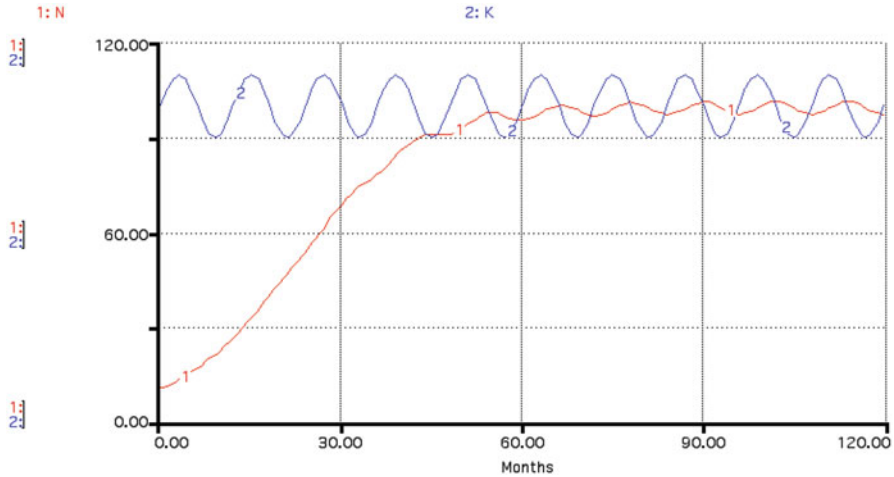


Fig. 2.4

How will this change in the carrying capacity over time affect the population size N . Since the carrying capacity has only little influence on N as long as N is small, we would expect the change in K not to alter the early sigmoidal growth phase of N . However, as N gets larger, K has an increasing influence on the subsequent changes in N . When you run the model, you should find that this is indeed the case. Look closely at the graph and recognize, however, that the changes in N and K are not exactly in sync with each other. Rather, an increase in K is not instantly matched by an increase in N . Can you explain why?

Again, explore the dynamics of the system by successively running the model for alternative specifications of R , K and initial population sizes. For example, enlarge the range over which K fluctuates over the course of a year. Alternatively, abandon the assumption that K fluctuates along a sinewave and make it a random variable. You can do so with the built-in function `RANDOM` which requires that you specify upper and lower bounds. For example, specify

$$K = 100 + \text{RANDOM}(-10, 10) \quad (2.3)$$

and K will fluctuate randomly between the values 90 and 110. Figure 2.5 shows the results of one model run with K specified as in Eq. (2.3). The time paths of this system are different from run to run because of the random number.

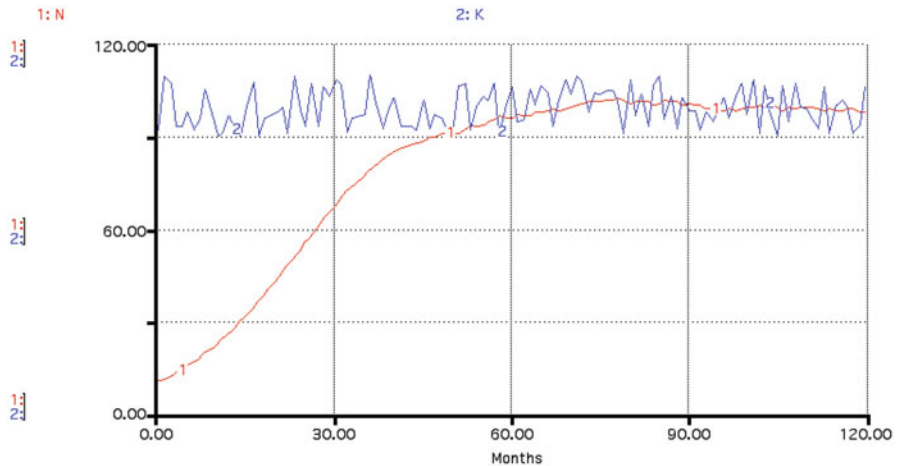


Fig. 2.5

2.4 Population with Varying Carrying Capacity Model Equations

$$N(t) = N(t - dt) + (\Delta N) * dt$$

$$\text{INIT } N = 10$$

INFLOWS:

$$\Delta N = R * N * (1 - N/K)$$

$$K = 100 + \text{SINWAVE}(10, 12)$$

$$R = .1$$

2.5 Sensitivity and Error Analysis with STELLA

Let us reflect for a moment on the models that we developed so far. We have hypothesized about the workings of a dynamic system—the influences on births and deaths in a population, and possible fluctuations in the maximum number of individuals of that population that can be sustained in a given environment. We have not concerned ourselves with real data describing real populations in a real environment. Rather, we were interested in the general features of such systems.

The modeling approach that we chose here is distinct from a data-driven, statistical approach. Statistical, or as they are sometimes called, empirical models are a kind of disembodied representation of some well-studied phenomenon. They have no connection to reality other than the purely mathematical. The systematical alternative, the kind we have used in this and similar books [1–3], strives to

represent as much as possible the reality of the dynamic phenomenon. Some refer to this form of modeling as the mechanical approach, but this term seems to us too wooden and likely to leave the impression that we think nature is just another mechanical process, rather like the engine of an auto. We do not think so.

In systematical modeling, we build into the representation of the phenomenon that we know actually exists—such as the birth and death processes of populations. Our systematical alternative therefore starts with an advantage over the purely statistical or empirical modeling schema. This advantage allows the systematical model to be used in more related applications than the empirical model—the systematical model is more transferable to new applications. But the empirical model does have one advantage: in the process of evaluating the data gathered about the phenomenon, the mean and standard deviations of the coefficients are found. The corresponding parameters and initial values in our models are not so elaborated. Such values are at first usually found or derived from the pertinent literature, often without a given variation.

Once the systematical model has performed to meet a general sanity test, the parameters and initial values need to be flexed to determine the sensitivity of the model results with regard to the choice of parameters and initial conditions. This process is time consuming and is usually allocated to the drudgery part of modeling. But it is essential. Just how effective is a model that responds with dramatic difference when one of its parameters is changed slightly? The point is not whether sensitivity analysis needs to be done but how can it be done efficiently? Our view is that STELLA is a very efficient tool for building the structure of the systematical model and for performing sensitivity analyses.

To conduct a sensitivity analysis, for example on the parameter R of our population model, choose “Sensi Specs...” (Sensitivity Specification) from the Run pull-down menu, and choose the parameter R —by clicking on it and selecting it—as the one for which you want to perform a sensitivity analysis. Type in the dialogue box “# of Runs” 5 to generate five sensitivity runs. Then provide start and end values for R . If you chose “Incremental” as the variation type, STELLA calculates the other values from the start and end values that you specified such that there are equal incremental changes in A from run to run. Plot the five resulting curves for N in the same graph by choosing the “Graph” option in STELLA II’s Sensitivity Specs menu. Run the model with the S-Run command and observe the resulting graph. Here are the results for R varying from run to run incrementally between 0.05 and 0.15, and a carrying capacity that is specified as

$$K = 100 + \text{SINWAVE}(10, 12) \quad (2.4)$$

The results of this model are shown in Fig. 2.6. Here, we have created one page in our graph pad that summarizes the five consecutive runs. You can do this by clicking on the graph that already existed, then selecting a new page for that graph pad by clicking the triangle that is labeled “New”, and then specifying that this should serve as a “Comparative” graph (see Fig. 2.7).

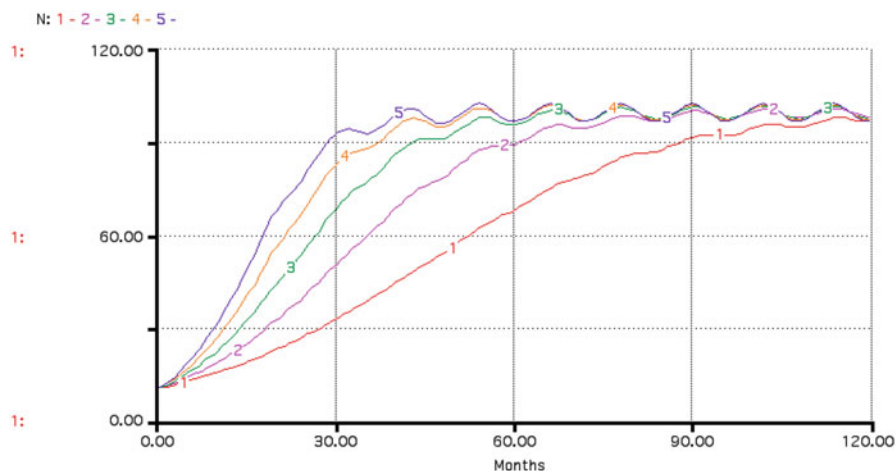


Fig. 2.6

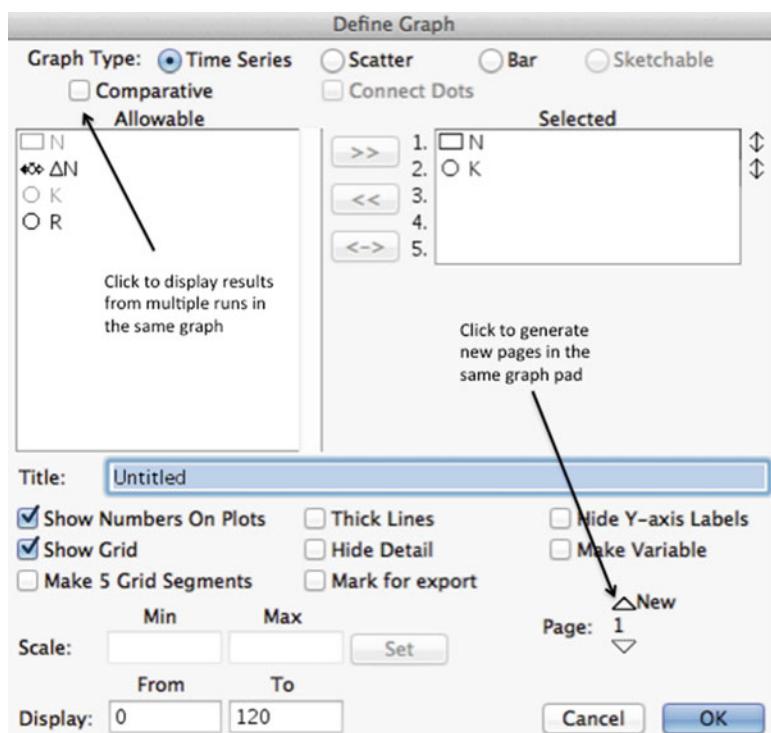


Fig. 2.7

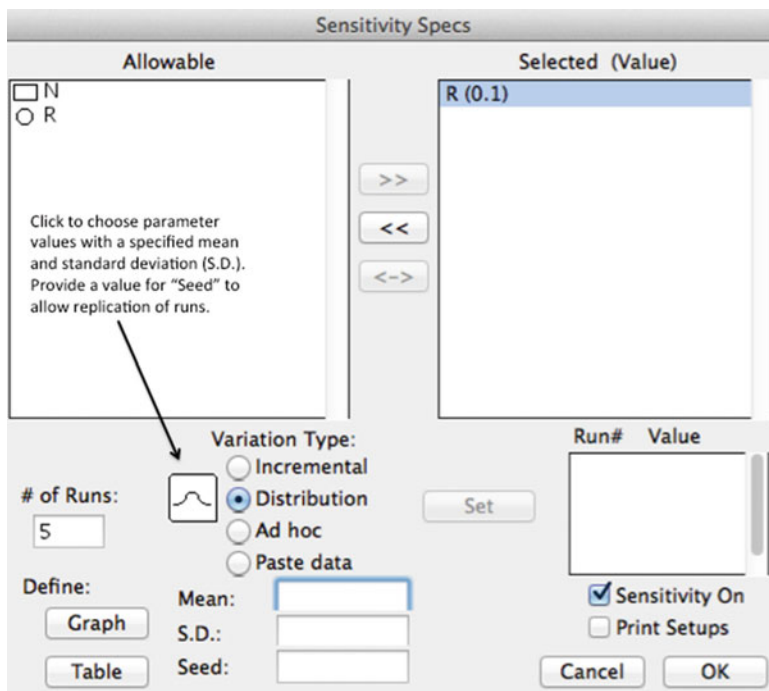


Fig. 2.8

If you wish to let values of R vary from run to run along a normal distribution with known mean and standard deviation, choose, within “Sensi Specs” the “Distribution” option instead of “Incremental”. When you specify “Seed” as a positive integer, you ensure that the model will replicate a particular random number sequence in subsequent sensitivity runs. Specify 0 as the seed and a “random” seed will be selected (Fig. 2.8). If you do not wish to make use of the normal distribution of the random numbers used in the sensitivity analysis, click on the bell curve button. This curve bell-shaped button will change its appearance when you click on it, and then allow you to specify a minimum, maximum and a seed for your sensitivity analysis.

Another choice for the specification of sensitivity runs in STELLA is not to change parameters in incremental intervals or along distributions. You can specify ad hoc values for each of the consecutive runs.

You can easily specify a whole series of parameter variations in STELLA and make the hundreds of runs needed to reasonably explore the combinations for their collected sensitivity. Examination of the results can lead you to those parameter groups that can cause trouble. You might consider eliminating such a combination by a structural change in the model or by investing more effort in narrowing the real range of these parameters through extended research.

Another rather interesting approach is to change each of the parameters to a sine or cosine function varying the mean value of the parameter, similar to what we have done in the preceding section of this chapter. Each parameter is assigned its own frequency and the model is run with all parameters and initial values varying in this way. A spectral analysis can be performed on the variations in the main variable with the hope of finding certain critical frequencies, leading you directly to the parametrical culprits.

Generally though, big computer-based models create a demand for big computers as they are needed to sift through the parameter and initial value specification problem. There is no easy way around this situation. The problem is actually larger than the parameter problem discussed here. There are many sources of modeling error. Gertner et al. [4] and Gertner and Guan [5] wisely advocate the use of Error Budgets as a way of pinning down the critical areas of error sources. He and his colleagues have developed the methods of breaking down the source of error in several categories (Input Measurement, Sampling, Components of the model (sets of equations), Grouping and Computational). They are able to isolate the sources of variation in the main variable. With such information the model can be effectively revised or the data collection effort intelligently redirected.

For very large spatial dynamic models with thousands of cells, the testing problem is very great, seemingly impossibly large. But efficient testing algorithms have been and are being developed.¹

In presenting your models and their results, you should always include the variations in the main variables of interest with changes in the critical parameters. This display reveals to the critical observer that you have a respect for the trouble that can be caused by what is still unknown about the process you study. The best thing that can happen to modelers is to have one of their models used to aid important decision-making. No good decision maker will use a model that has not been screened for its error potential.

2.6 Difference and Differential Equations

Let us more closely investigate how STELLA treats the equation we specify in our models. If we set $DT = 1$, then state variables are updated every full time period, such as every year, month or week. In this case, we have a model of discrete time. As DT is lowered, we still have a discrete time model, but more closely approach the case of continuous time. The model of this section illustrates the differences between the two cases.

¹ For a review of this approach and the general strategy of developing, sensitivity testing and using these large spatial models, see: <http://ice.gis.uiuc.edu>, generally and: <http://ice.gis.uiuc.edu/TortModel/tortoise.html>, specifically for the error budgeting process.

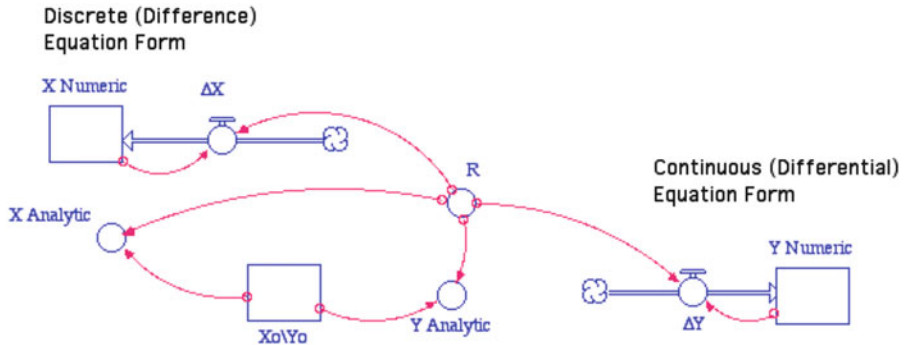


Fig. 2.9

Start with the following difference equation:

$$X(t+1) = R * X(t) \quad t = 1, 2, 3, 4 \dots \quad (2.5)$$

The analytic solution to this equation is:

$$X(t) = X_0 * R^t \quad t = 1, 2, 3, 4 \dots \quad (2.6)$$

In STELLA, this difference equation is

$$\Delta X = X(t+1) - X(t) = (R - 1) * X(t) \quad (2.7)$$

which yields what we term Y Numeric in the model of Fig. 2.9.

The continuous form version of this phenomenon is:

$$\Delta Y = R * Y, \quad (2.8)$$

yielding Y Numeric.

The analytic solution to this continuous time equation is:

$$Y(t) = Y_0 * \text{EXP}(R * t) = Y \text{ Analytic}. \quad (2.9)$$

X Numeric and X Analytic are the same if $DT = 1$. As DT approaches 0, these equations drift apart. But the analytic solution to the difference equation is good only for $DT = 1$ (Fig. 2.10). Conversely, when $DT = 1$, the Y Numeric and Y Analytic are far apart. Run the model with a $DT = 1/1024$, and you will find that numeric and analytical equations converge, as of course they should.

Figure 2.11 shows how much the two numeric solutions agree at $DT = 1$. Thus there is a substantial difference between the difference and differential (discrete vs. continuous) equations when they result in exponential solutions.

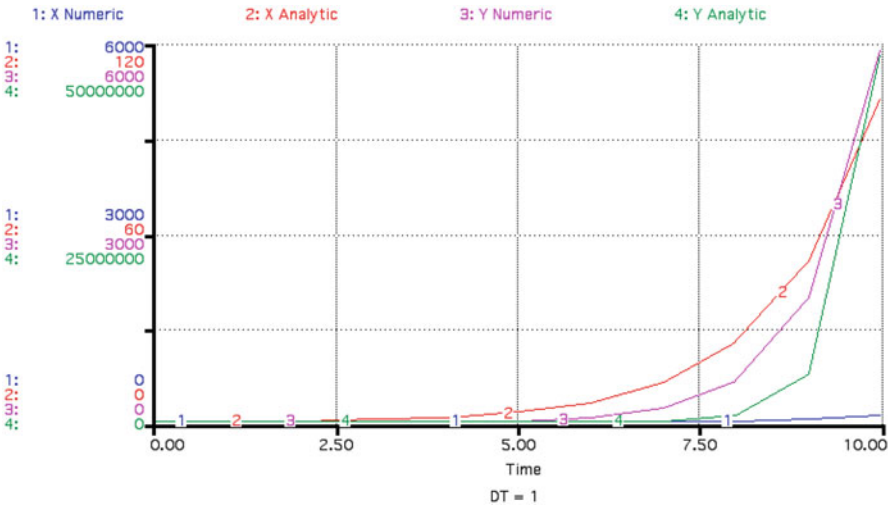


Fig. 2.10

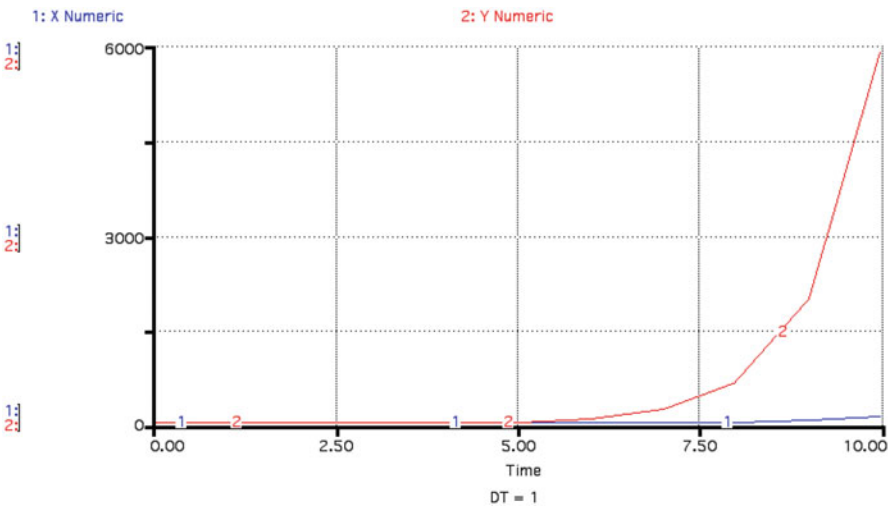


Fig. 2.11

2.7 Difference and Differential Equation Model Equations

$$\begin{aligned} X_o\backslash Y_o(t) &= X_o\backslash Y_o(t - dt) \\ \text{INIT } X_o\backslash Y_o &= 0.1 \\ X_Numeric(t) &= X_Numeric(t - dt) + (\Delta X) * dt \\ \text{INIT } X_Numeric &= X_o\backslash Y_o \end{aligned}$$

INFLOWS:

$$\Delta X = (R-1)*X_Numeric$$

$$Y_Numeric(t) = Y_Numeric(t - dt) + (\Delta Y) * dt$$

$$\text{INIT } Y_Numeric = X_0 \backslash Y_0$$

INFLOWS:

$$\Delta Y = R * Y_Numeric$$

$$R = 2$$

$$X_Analytic = X_0 \backslash Y_0 * R^{\text{time}}$$

$$Y_Analytic = X_0 \backslash Y_0 * \text{EXP}(R * \text{time})$$

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