

# Phaser Module: Ricker Salmon Model

## Will the Salmon Obey Ricker?

### Highlights:

*The justification for using any reproduction curve must in the long run come from observation.*'' – W.E. Ricker (1954)

The Ricker model, a scalar difference equation with density-dependent growth, is one of the most widely known models for modeling fish populations. The goal of this project is to determine if the actual salmon population data obtained from the [USACE's](#) Columbia and Snake River project can be described by the Ricker model. First, the parameters that influence the salmon population model are estimated from this data using elementary statistical methods. Then, using these parameter values, the dynamics of the model are explored with Phaser.

### Equation:

$$N_{t+1} = N_t e^{r(1-N_t/p)}$$

Variables:

$N_t$  : Population at time t (the current generation)

$N_{t+1}$  : Population at time t + 1 (the next generation)

Parameters:

r : Growth rate of the population

p : Carrying capacity

### Discussion:



Let us begin our discussion with an explanation of the suitability of Ricker's difference equation above for modeling salmon populations. There are two key considerations in deriving an equation to describe a salmon population:

1. Salmon populations have non-overlapping generations. Their [life cycle](#) involves the adults leaving the river before the offspring are born, meaning that only one generation inhabits the river at each moment in time. Naturally, the size of each generation is a function of the size of the previous generation from which it was produced. Therefore it is best to use a difference equation of the form

$$N(t+1) = N(t) f(N(t)),$$

where the next generation  $N(t+1)$  is a function of the previous one  $N(t)$  and  $f(N(t))$  is a density-dependent growth rate.

2. The next task is to determine an appropriate form of the growth rate function  $f(N(t))$ . The Ricker model assumes exponential growth when the population is small; the fish have ample resources and can reproduce at an exponential rate. However, the exponential model of population growth needs to be modified because, "...density-dependent causes of mortality set a limit to the size which a population achieves (Ricker, 619)." For example, the Ricker model consists of an exponential term that is modified by factors relating to predation and the negative effects of overcrowding. In this way, the population is controlled by a negative feedback mechanism, "turning off" the population growth and reversing it when it becomes too large.

Therefore, based on the assumptions of proportionality between generations and the exponential growth/decay of the population, the final expression is

$$N_{t+1} = N_t e^{r(1-N_t/p)}$$

Here, the parameter  $r$  (positive) controls the growth rate and  $p$  (positive) controls the carrying capacity. Note that the exponential growth factor is larger than 1 when the population size is above the carrying capacity; and it becomes less than 1 when the population size is above the carrying capacity.

You can find further biological and mathematical details of a derivation of this model in (Ricker 1954) and (Greenwell 1984).

### Salmon data from John Day Dam:

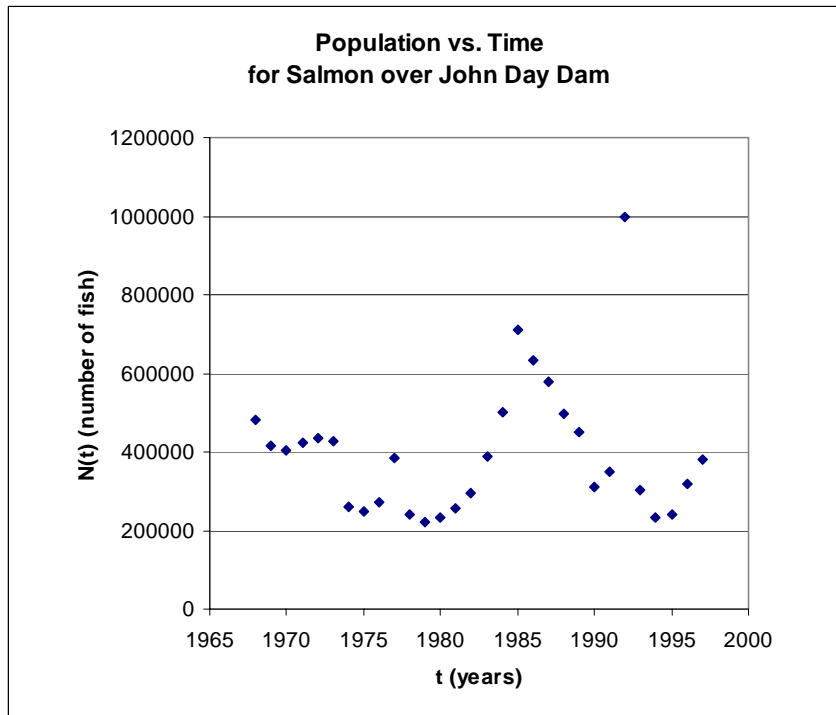
In this module, we will use the data for the salmon population over John Day Dam. There are several species of salmon for which we have enough data to model: coho, chinook, sockeye, and steelhead.



The data set we consider in this module represents the total salmon counted over the John Day Dam, not divided into different varieties. More in-depth data concerning these different varieties of salmon and different dams are available in the experimental data section of this module.

In preparation for our theoretical study of the John Day Dam total salmon count, let us take a close look at the data in several different ways.

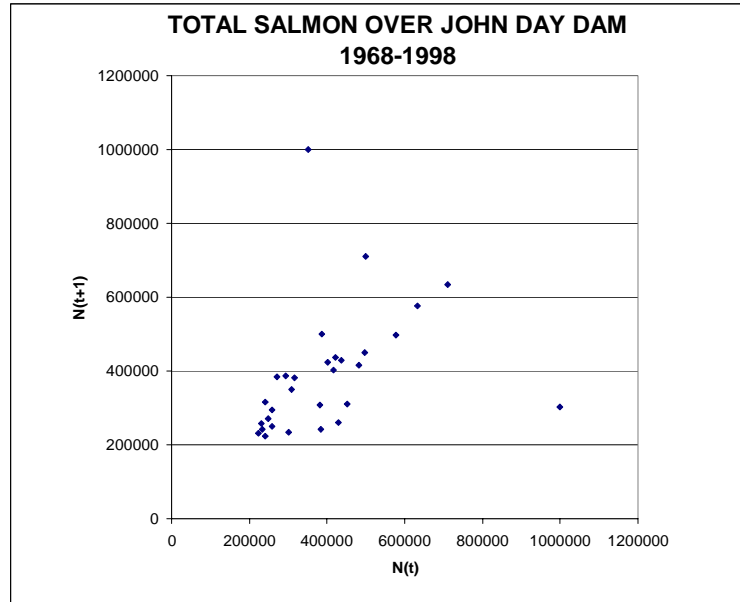
**N(t) vs. time t:** In Figure 1, we have plotted the number of fish  $N(t)$  against time  $t$  for about 30 years.



**Figure 1.** Salmon count per year over the John Day Dam. Data points and their graph are available in a Microsoft Excel file under this [link](#).

As can be expected from real data, the salmon population does not appear to follow a recognizable pattern over years. In fact, it is difficult to extrapolate into the future and try to guess how the data might evolve over a longer time period.

**N(t+1) vs. N(t):** Recall that one of the assumptions of the model is that the next generation is a function of the current one. In an attempt to see this functional relationship of two succeeding generations, we now plot  $N_{t+1}$  against  $N_t$  in Figure 2.



**Figure 2.** Salmon data plot: current generation vs. next generation.

As Ricker comments in his abstract, “Plotting net reproduction (reproductive potential of the adults obtained) against the density of stock which produced them, for a number of fish and invertebrate populations, gives a domed curve whose apex lies above the line representing replacement reproduction. At stock densities beyond the apex, reproduction declines either gradually or abruptly (559).” Based on this description, we have some possible expectations for the shape of this curve. Looking at Figure 2, however, it is unclear what kind of “domed curve” we could expect to fit to the scatter plot.

**Estimation of parameters from data:**

With the qualitative description of the data in mind, let us get more specific about how we can estimate the values of the two parameters  $r$  and  $p$  from the data. For this purpose, we manipulate the model equation following the steps below:

<u>Model</u>	<u>Comments</u>
$N_{t+1} = N_t e^{r(1-\frac{N_t}{p})}$	Ricker Model
$\frac{N_{t+1}}{N_t} = e^{r(1-\frac{N_t}{p})}$	Rewrite Ricker Model
$\ln \frac{N_{t+1}}{N_t} = r(1 - \frac{N_t}{p})$	Take the natural logarithm of both sides
$\ln \frac{N_{t+1}}{N_t} = r - \frac{r}{p} N_t$	Distribute $r$ over the parentheses

$$\ln \frac{N_{t+1}}{N_t} = \frac{-r}{p} N_t + r \quad \text{Re-arrange the result into a linear form}$$

In the final arrangement of the Ricker equation above, observe that we have the

$$y = m x + b$$

form of a linear equation, with

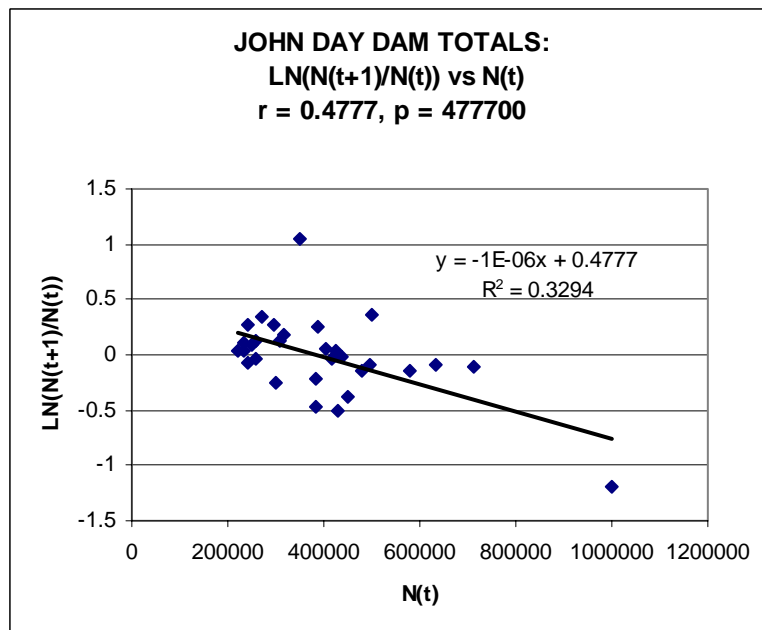
$$y = \ln \frac{N_{t+1}}{N_t}, \quad x = N_t$$

where

$$m = \frac{-r}{p} \quad (\text{slope}), \quad \text{and} \quad b = r \quad (\text{y-intercept}).$$

Writing the model in this form is a powerful tool. We can plot  $\ln \frac{N_{t+1}}{N_t}$  versus  $N_t$  and try to fit a trend line through the data points. From the y-intercept and the slope of such a trend line we can estimate the values of the model parameters  $r$  and  $p$ .

**r and p for John Day Dam data:** In Figure 3 below, we have first plotted  $\ln \frac{N_{t+1}}{N_t}$  versus  $N_t$  as a scatter plot using the data from Figure 2 for the John Day Dam. Then using Microsoft Excel program, we have determined the best trend line for the scatter plot.



**Figure 3.** Estimating r and p from a trend line. Data points and the computation of the trend line are available in a Microsoft Excel file under this [link](#).

From this graph, the values of r and p for this population of salmon can be determined, since r is read directly as the y-intercept and p is r divided by the slope:

$$r = 0.4777 \quad \text{and} \quad p = 477700.$$

If the data fit the model perfectly, then the points should all line up to form a straight line with slope equal to  $\frac{-r}{p}$ . Excel's  $R^2$  value can be used to determine how close the data are to fitting the trend line

(for additional details follow this [link](#)). Note that the r and p values determined from this line contain a considerable amount of error since the trend line itself is only an approximation.

## Dynamics:

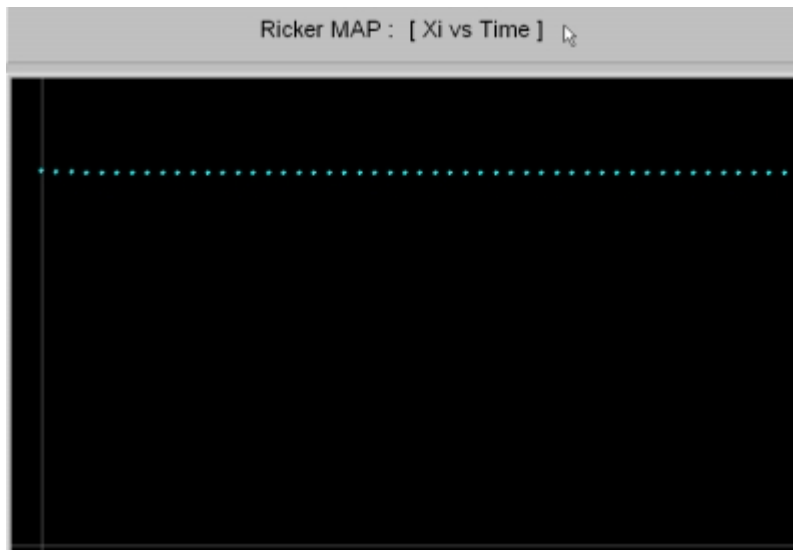
Equipped with the values of r and p above, the dynamics of the model can now be simulated in Phaser. We will present several such simulations and compare them with the data plotted in Figures 1-3 above. Note: The difference equation of Ricker is entered into Phaser as

$$x1 \rightarrow x1 * \exp(r * (1 - x1/p)).$$

Therefore, it is important to make the notational translation that  $N(t)$  is  $x1(t)$  in the Phaser simulations and screen images below.

**Xi vs. Time:** In Figure 4, we have plotted the predicted salmon count for the John Day Dam from the Ricker equation.

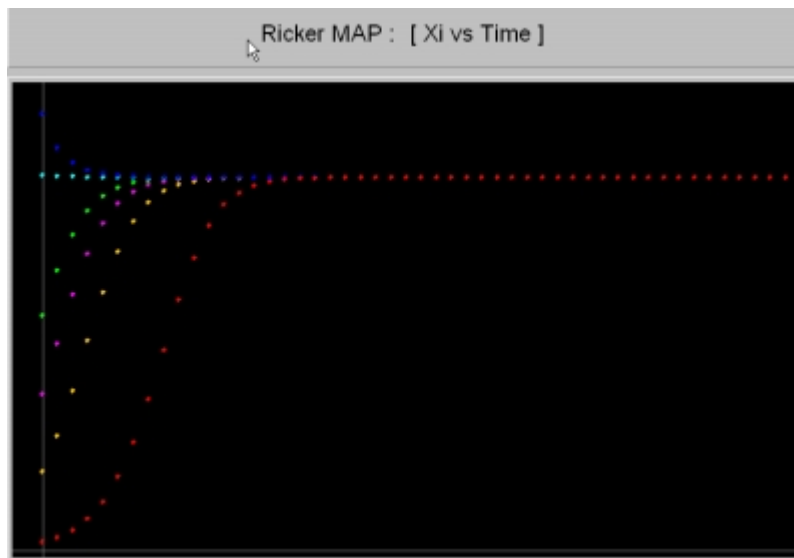
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**Figure 4.** Phaser simulation of 60 generations of the total salmon population for the John Day Dam. You can load this Phaser simulation (a **Phaser Project File**) into your local copy of Phaser by clicking on the picture or [here](#).

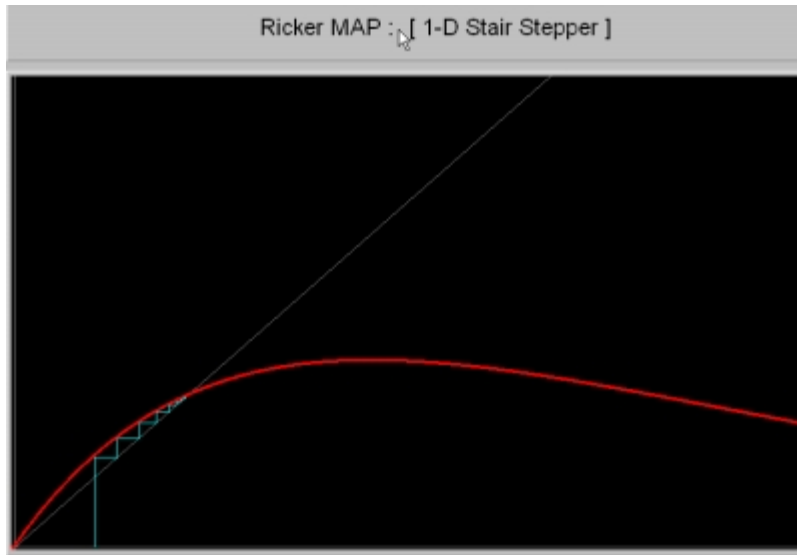
From Figure 4,  $X_i$  vs.  $t$  plot, we can see that as time goes on, the population ( $X_i$ ) approaches a carrying capacity of 477700. The plot in this figure is for the initial condition obtained from the experimental data for the year 1968 (the first year for which we have data), and since this initial condition of 480990 is rather close to the equilibrium value, the graph appears almost as a straight line. It is evident that the prediction in Figure 4 has no resemblance to the data in Figure 1.

We can also simulate what would happen if we choose different initial conditions (different initial population sizes) for the same fixed values of the parameters  $r$  and  $p$ . It is evident from Figure 5 below that with a variety of initial conditions, the populations eventually reach the same carrying capacity, unless of course you start with a zero population size, in which case the population would remain zero for all future time.



**Figure 5.** Regardless of the initial population size, the salmon population eventually reaches the same level (carrying capacity). You can load this Phaser simulation (a **Phaser Project File**) into your local copy of Phaser by clicking on the picture or [here](#).

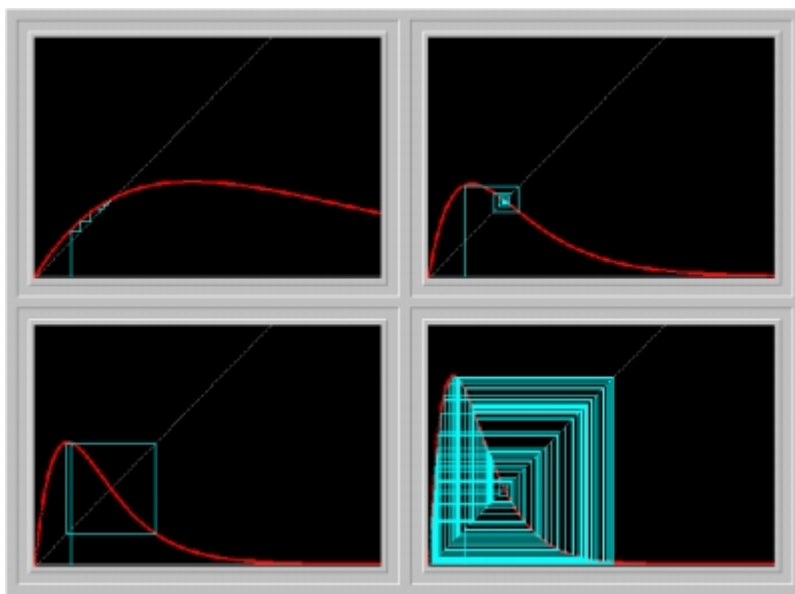
**Stair-Step Diagrams:** Next, we plot in Phaser the “domed shaped reproduction curve” and a representative solution of the model for the estimated parameter values. We accomplish this using the Stair-Step diagram plotting facility of Phaser. To find out more about how these diagrams are computed and their interpretations, you can consult the Tutorials in PhaserHelp, or Chapter 3 of (Hale and Kocak 1991).



**Figure 6.** The “reproduction curve” (red) and the stair step diagram of the salmon population over John Day Dam. You can load this Phaser simulation (Phaser Project File) into your local copy of Phaser by clicking on the picture or [here](#).

The stair-stepper plot shows that the population is approaching an asymptotically stable fixed point (477700) at the intersection of the red reproduction curve and the 45-degree line. This value is the carrying capacity for this population according to the Ricker model.

**A Gallery of  $r$  values:** Small variations in the parameters  $r$  and  $p$  do not change the qualitative dynamics of the model very much. However, large changes in the growth rate parameter  $r$  can result in oscillatory, even chaotic, dynamics in the model. In Figure 7, we display a Gallery of Phaser simulations for four values of  $r$  while the other parameter  $p$  is fixed.





**Figure 7.** A Gallery of salmon populations for the parameter values  $r = 0.477, 1.75, 2.3,$  and  $3.0,$  while  $p = 4770000.$  You can load this Phaser simulation (a **Phaser Gallery File**) into your local copy of Phaser by clicking on the picture or [here](#).

Notice that as the parameter  $r$  is increased, the hump of the reproduction curve becomes more pronounced. The stable fixed point of the model becomes unstable ( $r > 2$ ) and the dynamics turns oscillatory with period 2. As seen in the last frame of the Gallery, the dynamics becomes eventually unpredictable (chaotic) when the parameter  $r$  gets sufficiently large. You should consult the general Ricker Model for further information about the fascinating dynamics and bifurcations of the Ricker model.

The pictures above are interactive, so try experimenting with different situations to test the assertions we have made about the model's dynamics.

## Experimental Data:

Salmon population data for this module was obtained from the U.S. Army Corps of Engineers' [Annual Fish Passage Report](#). The report includes fish counts as well as other data related to the USACE's project monitoring eight dams on the Columbia and Snake Rivers.

The project's goal is to improve salmon passage through the dams, which originally prevented salmon from spawning and put many of them on a list of threatened species. Although the achievement of this goal has not been one hundred percent, several structural improvements have allowed the salmon populations to attain some stability over the span of the project. More information about the Columbia and Snake River project can be found on the USACE's [Fish Management Office](#) website.

Of the six dams studied, salmon data for the John Day Dam fit the Ricker Model better than data collected at other dams. However, the value of  $R^2$  for the total salmon population over John Day Dam is 0.3294, indicating that it is a loose fit at best. To see how data from the other dams fits the Ricker Model, we have performed these analytical steps for the data at all six dams. To view the complete data set for a particular dam in a MS Excel workbook, click on one of the links below:

[Bonneville Dam](#)  
[Ice Harbor Dam](#)  
[John Day Dam](#)

[Lower Monumental Dam](#)  
[McNary Dam](#)  
[The Dalles Dam](#)

**Acknowledgement:** We thank the US Army Corps of Engineers Northwest Division for their permission to use their salmon data, as well as several pictures, from their Web site without which this module would not have been possible.

## Critique- For and Against:

In 1954, W.E. Ricker realized that "... it has become an urgent problem to have a scientific description of the regulation of abundance of fish stocks, in order to complete the basis for predicting optimum levels of exploitation (560)." This urgency still persists today. Due to their continuously declining numbers, salmon populations in the Pacific Northwest must be managed in an ecologically sound way. Theoretical models based on experimental data are central for sustainable harvesting of salmon stocks.

### For:

- ➡ The Ricker model is historically a significant one in modeling populations with non-overlapping generations. Every student of quantitative ecology should be aware of it.
- ➡ It is possible to see general relationships between the experimental data and the data predicted by the model, such as the negatively sloping linear relationship of the natural log plots, which shows that, at least, the basic assumptions of the model are plausible.

### Against:

- ➡ In analyzing the salmon data from six of the dams along the Columbia and Snake rivers in this fashion, we discover that, in general, the Ricker model does not describe these populations with much accuracy. Indeed, in his 1954 article, "*Stock and Recruitment*," in reference to the Pink salmon, Ricker himself acknowledges that "*No very clear idea of the shape of the reproduction curve can be obtained (p589).*"
- ➡ The model does not reflect outside influences on the salmon populations, such as dams or other man-made impediments, pollution, unnatural rates of harvesting, or random variation, but rather assumes a rather pristine natural environment. A further study of this model accounting for these effects could yield more precise results.

### Suggested Explorations:

1. If you do not have access to Microsoft Excel, or just want to do your own parameter estimation using a different program, total salmon population data for the John Day Dam is available as a text file [here](#).
2. Load the Phaser project files in Figure 5 and 6, and explore the dependence of dynamics on small changes in  $r$  and  $p$ . Do you notice any qualitative changes if you vary the parameters, say, 10 percent? Do all solutions still approach a stable equilibrium state?
3. Can you generate a  $X_i$  vs. Time plot by trying different parameter values so that it resembles the data plot in Figure 1?
4. Compute the  $r$  and  $p$  values using the data for any one of the dams listed in the Experimental Data section. Check your answers by following the link to the [r and p constant table](#). Now, using your parameter values in Phaser, generate a  $X_i$  vs. Time plot. Does this plot resemble the observed fish data?
5. Load the Phaser gallery file in Figure 7, and explore the dependence of dynamics on the parameter  $r$ . Notice that for  $r = 2.3$ , the Ricker model predicts stable oscillations. Can you determine the smallest value of  $r$  for which oscillations persist?
6. In the Ricker equation set the parameter values to  $r = 2.3$  and  $p = 3.0$  and generate 100 data points using Phaser (you can save the  $x_i$ -values to a file in Phaser). Using the parameter estimation method described above, see how close you can come to the values of the parameters you have set. You can repeat this experiment with several initial conditions.

7. Verify that  $N(t) = p$  is a fixed point of the Ricker equation. Linearize the equation about this fixed point and deduce that it is asymptotically stable for  $r < 2$ .

## Related Modules:

Generalized Ricker Model

## References:

Adult Fish Counts. Contact: Marie Kopka. 2004. U.S. Army Corps of Engineers, Portland District, Operations Division, Natural Resource Management Section. 30 January 2004

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Endangered Species Act Status Reviews and Listing Information. 2004. NOAA Fisheries, National Marine Fisheries Service. 31 March 2004

<http://www.nwr.noaa.gov/1salmon/salmesa/>

GREENWELL, R. N. and NG, H. K. "Ricker Salmon Model." *UMAP Journal* Vol. 5, No. 3 (1984): 337-362.

HALE, J. and KOCAK, H. *Dynamics and Bifurcation*. Springer-Verlag, New York. (1991).

RICKER, W.E. "Stock and Recruitment." *Journal of the Fisheries Research Board of Canada*, **11** (1954): 559-623.

USACE Northwest Division Fish Management Office. Contact: Adele Merchant. August 27, 2004.

<https://www.nwd.usace.army.mil/ps/>

## Feedback:

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