# Module 653

## The Ricker Salmon Model

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| TITLE: | THE RICKER SALMON MODEL |

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MATH FIELD:    Difference equations

APPLICATION FIELD:    Ecology

TARGET AUDIENCE:    Students in a differential equations or modeling course.

ABSTRACT:    A difference equation model describing the dynamics of a salmon population was developed by W.E. Ricker in 1954. This unit derives the model, shows how it can be modified, and introduces the concept of maximum sustainable yield. It also shows how difference equations may lead to periodic and chaotic behavior, and a computer program enables one to explore the periods and chaos. The technique of dynamic programming is introduced to show how to maximize the income from fishing over a finite period.

PREREQUISITES:    Elementary differential equations.

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## Modules and Monographs in Undergraduate Mathematics and its Applications Project (UMAP)

The goal of UMAP was to develop, through a community of users and developers, a system of instructional modules in undergraduate mathematics and its applications to be used to supplement existing courses and from which complete courses may eventually be built.

The Project was guided by a National Advisory Board of mathematicians, scientists, and educators. UMAP was funded by a grant from the National Science Foundation and is now supported by the Consortium for Mathematics and Its Applications, Inc. (COMAP), a nonprofit corporation engaged in research and development in mathematics education.

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The project would like to thank all those who assisted in the production of this unit.

# 1. Introduction

In the Pacific Northwest, the economic survival of many people hinges on the success of the salmon fisheries, which in turn depends upon the survival of the salmon (who wouldn't mind surviving, either). The fishermen would like to maximize their profits by catching as many salmon as possible, but excessive fishing could cause the salmon population to drop so low that the future of the industry would be jeopardized.

Mathematical models have been used to help determine fishing policy. If a model accurately describes the biological situation, it can provide us with information otherwise difficult to obtain, as well as confirm observations already made. Further, it can suggest new areas for biological observation.

One of the most widely used mathematical models for salmon fisheries was developed by W.E. Ricker in 1954 [11]. In this unit, we will derive the Ricker model, using a derivation simpler than that of Ricker. We will then salmon up our calculus skills to study some properties of the model and make some conclusions. Next, we will exsalmon how this rather simple model exhibits some very complex and chaotic behavior under certain circumstances. Finally, we will introduce a technique known as dynamic programming to derive additional information from the model.

# 2. The Life of a Salmon

We start this story in the middle of the salmon's career, when they are swimming in the ocean, growing in size and strength. After a few years of the good life, the salmon start an arduous journey upstream to their birthplace. Guided by some unknown mechanism, they swim hundreds of miles against the current, making heroic leaps over rocks and waterfalls. When they finally reach their spawning place, the female salmon lay their eggs, which are then fertilized by the male salmon. At this point, the salmon have lost a quarter of their body weight, having fasted during their long journey. They soon die in the same water in which they were born.

A few months later the eggs hatch, and the baby salmon emerge. They are vulnerable at this stage to predatory birds and fish, which would love nothing better than to gobble them up. When the survivors become large enough, they begin their journey back to the ocean, where the life cycle begins all over again, repeating the odyssey of the previous generation.

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# 3. Derivation of the Model

Since one generation of salmon dies before the next appears, we will use a difference equation to express the population of any generation in terms of the previous one. In contrast, many population models assume a continuous change in population, and so use a differential equation.

Our model requires six assumptions. We begin with two: first, the number of eggs laid is proportional to the number of adult salmon; and second, the population of the next generation is proportional to the number of eggs laid. These assumptions seem fairly reasonable, and when we put them together we get

$$N_{t+1} \propto N_t, \tag{1}$$

where $N_t$ is the population in year $t$ and $N_{t+1}$ is the population in year $t+1$. As we shall later see, this relationship is not your usual proportion, because the "constant" of proportionality varies with $N_t$.

If this were the whole story, the salmon population would increase exponentially; that is, we would have $N_t = N_0 k^t$, where $k$ is the constant of proportionality.

**Exercise 1.** Prove this last statement.

But this unbridled growth is limited by the birds and other fish who prey upon the young salmon. Our third assumption is that, until they reach a certain size, salmon are eaten at rates proportional to their number. If we let $R$ be the population of the new generation, known as recruits, then

$$\frac{dR}{dt} = -cR, \tag{2}$$

where $c$ is a constant or proportionality. Notice that we use a differential equation here, since $R$ is large and the predation is going on continuously over a period of time. Solving Eq. (2), we get

$$R = R_0 e^{-ct}, \tag{3}$$

where $R_0$ is the initial recruit population.

**Exercise 2.** Derive Eq. (3).

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Our fourth assumption is that after a time $T$, the young salmon become too big for most predators to swallow, and so their population stops decreasing. Our fifth assumption is that $T$ is proportional to the number of eggs laid, which we already assumed to be proportioned to $N_t$, the adult population. The rationale here is that if there are twice as many baby salmon, and they have the same amount of food to go around, it will take twice as long for them to reach that critical size at which they can no longer be eaten easily. This assumption may seem less plausible than the others, but it is not too far-fetched, and a more reasonable assumption may make our model too complex to analyze. So we will assume

$$T = KN_t ,\qquad\qquad(4)$$

where $K$ is another constant of proportionality. Putting $T$ in for $t$ in Eq. (3) yields

$$R = R_0\, e^{-CKN_t}.\qquad\qquad(5)$$

Finally, we assume that the number of adults in the next generation is proportional to the number of recruits, as given in Eq. (5). Putting this together with Eq. (1), we have

$$N_{t+1} \propto N_t\, e^{-CKN_t},\qquad\qquad(6)$$

since, for $N_{t+1}$ to be proportional to two quantities, it must be proportional to their product. We will let the constant of proportionality be $e^r$, so that (6) can be rewritten as

$$N_{t+1} = N_t e^r\, e^{-CKN_t} = N_t\, e^{r(1-(CK/r)N_t)}.\qquad\qquad(7)$$

Notice that if $N_t = r/CK$, then $N_{t+1} = N_t$, and hence all subsequent populations also equal $r/CK$. This is a special value of the population known as the *equilibrium population*, and we will denote this value by $P$. If the population ever exactly equals $P$, our model predicts that it will stay there forever. We will assume that $r$ is positive; otherwise the equilibrium population will not exist, and, in fact, the population will get smaller as time passes. We can then simplify (7) as

$$N_{t+1} = N_t\, e^{r(1-N_t/P)}.\qquad\qquad(8)$$

This is the form of the Ricker model we will usually work with.

Sometimes, rather than measuring the population $N_t$ directly, we will look at the fraction of the equilibrium population by

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denoting $X_t = N_t/P$. Then, when the population is at equilibrium, $X_t = 1$. Eq. (8) becomes

$$X_{t+1} = X_t e^{r(1-X_t)}. \tag{9}$$

Since our model is based on six assumptions, it is only as valid as those assumptions; a model is only a model and should not be confused with the real thing. Nevertheless, it is a first step toward a quantitative understanding of salmon population. When treated with caution, the results can be helpful.

# 4. Properties of the Model

Let us see what we can learn from the model. Denote $N_{t+1} = f(N_t)$, where

$$f(N) = N e^{r(1-N/P)}.$$

**Exercises 3.** Show that $f'(N) = (1 - r N/P) e^{r(1-N/P)}$.

4. Show that $\lim\limits_{N \to \infty} f(N) = 0$.

Looking at the result of Exercise 3, we see that when $N < P/r$, $f'(N) > 0$, so $f$ is increasing. Also, $f$ is decreasing when $N > P/r$. Thus, the population of the next generation is greatest when $N = P/r$. This value of $N$ is known as the *maximum recruitment level*. At this point we have $f(P/r) = (P/r) e^{r-1}$. Coupling this fact with the result of Exercise 4 and the fact that $f(0) = 0$, we can graph $f$ roughly as shown in Fig. 1.

In Fig. 1 we have also drawn a 45° line. Where it crosses the graph of $f$, $N = f(N) = P$. We have also drawn $P$ to the right of $P/r$, indicating $r > 1$. It is also possible to have $r < 1$ and $P/r$ to the right of $P$. The salmon population will grow if $f(N) > N$ (the part of the curve above the 45° line). Or we can catch all of the surplus population, $f(N) - N$, and be left with a population identical in size to the last generation. The fishing industry is interested in the population that will give it the maximum harvest of this type, so it can continue to harvest this same maximum harvest year after year. This is known as the level of *maximum sustainable yield*.
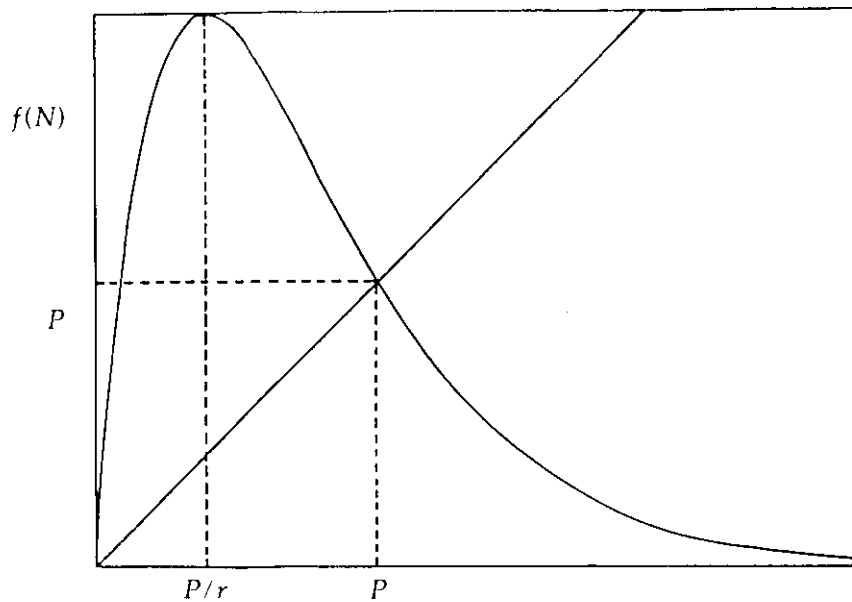
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Figure 1. The graph of $F(N)$ (population of the next generation) vs. $N$ (population of this generation).

**Exercise 5.** Show that the maximum sustainable yield occurs when $f'(N) = 1$.

We can call the value found in the last exercise $N^*$. We cannot determine $N^*$ analytically, but we can use a numerical scheme such as Newton's method if we already have values for $r$ and $P$. Once we know $N^*$, it is not hard to find the harvest.

**Exercise 6.** Show that the maximum sustainable yield is

$$N^* \left( \frac{1}{1 - rN^*/P} - 1 \right).$$

# 5. Do the Data Really Fit the Model?

That's a good question. Fig. 2 shows some of the data from [12].

We must admit, albeit with some disappointment, that we could fit almost any curve with equal success (or lack thereof) through this motley group of points in Fig. 2.
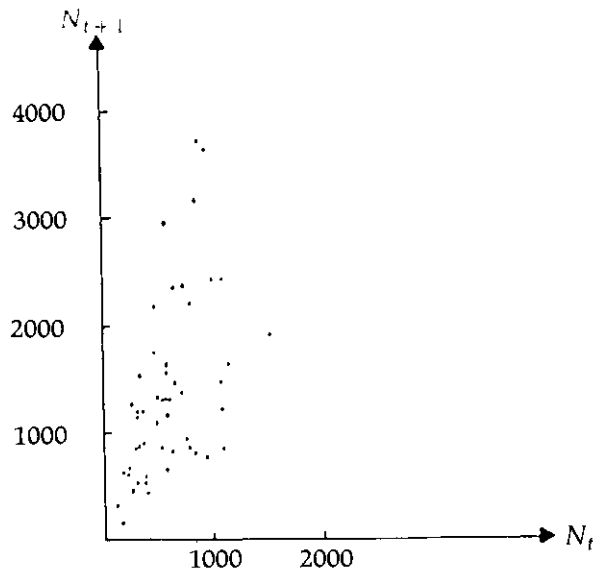
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Figure 2. The plot of $N_{t+1}$ vs. $N_t$ for data taken from [12].

Part of the problem is that our model is deterministic: the size of each generation is completely determined by the size of the previous generation. In reality, there are other factors, such as climate and food supply, which, as far as our model is concerned, are random variables. Some have suggested that a random factor be added to the model:

$$N_{t+1} = N_t\, e^{r(1 - N_t/P)\, + \, \sigma_t}, \tag{10}$$

where $\sigma_t$ is a normal random variable.

Another problem is that the model may need modification. Thomas et al. [13] found that data for fruit flies (which are not closely related to the salmon, although the salmon might make a nice snack out of them), fit the $\theta$ — Ricker model:

$$N_{t+1} = N_t\, e^{r(1 - (N_t/P)^\theta)}. \tag{11}$$

If $\theta = 1$, Eq. (11) reduces to the regular Ricker model in Eq. 8. It can be derived in a manner analogous to the derivation of the regular Ricker model by assuming that the time for the recruits to reach a less vulnerable size is proportional to the number of eggs laid, raised to the $\theta$ power. This is highly reasonable if $\theta < 1$, for it says that if the number of eggs laid is doubled, the rate that the young fruit flies (or salmon) grow should not be reduced by a full factor of two, due to a saturation effect. In the data from Thomas et al., $\theta$ is less than 1 in 52 out of 58 times. But then, these are not

salmon anyway, and before using this model to study fruit flies, we should see whether our original six assumptions are valid for fruit flies. (Ricker's original derivation used a different set of assumptions to arrive at the same model.)

The process of modifying a model, checking it against the data, and then modifying it again is typical in mathematical modeling, and the cycle can go on indefinitely. Each time through the cycle the model usually becomes more complex and difficult to analyze, while doing a better job of reflecting reality. But we will stop the cycle right now by staying with the original Ricker model through the rest of this unit.

A commonly used procedure to find $r$ and $P$, when presented with a series of populations $N_0$, $N_1$, ..., $N_n$, is to introduce a new variable $y_t = ln(N_{t+1}/N_t)$ and plot $y_t$ vs. $5_t$. If the original data fit the Ricker model (Eq. 8), then the plot of points $(N_t, y_t)$ should lie along a straight line.

**Exercise 7.** Find the equation of the line relating $y_t$ to $N_t$.

A technique known as the method of least squares can then estimate r and P. For more information on this method, see [1].

# 6. Chaotic Behavior

Suppose the salmon population at some time is close to, but not equal to, the equilibrium population $P$. It would be nice if the population gradually got closer to $P$, or at least didn't slip any further away. If, instead, the population does not approach its equilibrium value, we would like to know what it does instead. Depending on the value of $r$, the population may fluctuate randomly, with no apparent pattern. Furthermore, it turns out that this is true for any model $N_{t+1} = f(N_t)$ whose graph $f$ has a hump in it, as in Fig. 1.

For simplicity, let us use Eq. (9) rather than Eq. (8) for our model. Denote $X_{t+1} = F(X_t)$. Then the equilibrium point is $P = 1$. The equilibrium population $P$ is said to be *locally stable* if, when a value $X_t$ is close to $P$, the next value $X_{t+1}$ is no further away.



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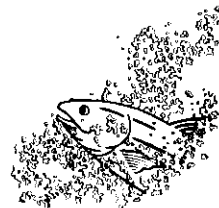
Mathematically, this says

$$|X_{t+1} - P| \leq |X_t - P| \tag{12}$$

or

$$\frac{|X_{t+1} - P|}{|X_t - P|} \leq 1.$$

But $X_{t+1} = F(X_t)$ and $P = F(P)$, so we have

$$\frac{F(X_t) - F(P)}{X_t - P} \leq 1. \tag{13}$$

If we take the limit (as $X_t$ approaches $P$) of the left hand side of this last inequality, we get $|F'(P)|$. If we require that $|F'(P)| < 1$, then the equality in (13) will be true for $X_t$ close enough to $P$, so we have local stability at $P$.

**Exercise 8.** Use this result to show that the equilibrium point in our model is stable if $r < 2$.

Actually, the equilibrium point is *globally stable* for $r < 2$. That is, $X_t$ approaches 1 as $t$ approaches infinity even if it doesn't start close to 1. (For a proof of this, see [3].) Some pictures may help explain this behavior. In Fig. 3, $|F'(1)| < 1$ and $X_t$ gradually moves toward 1. In Fig. 4, $|F'(1)| > 1$ and $X_t$ gets further from 1.

Notice in Figs. 3 and 4 how we start with $X_t$ on the $x$-axis, move vertically to find $F(X_t) = X_{t+1}$ on the graph, and then move horizontally to the line $y = x$ to find the corresponding point on the $x$-axis.

If we were to continue the process started in Fig. 4, we would find that $X_t$ does not continue to get further from 1. To see what is going on, let us look at what happens over two generations by examining $F(F(X_t)) = X_{t+2}$. If we plot $X_{t+2}$ vs. $X_t$ for values of $r$ slightly larger than 2, we will see something like Fig. 5, which uses $r = 2.3$. Let us call this new relation $F^{(2)}(X)$.
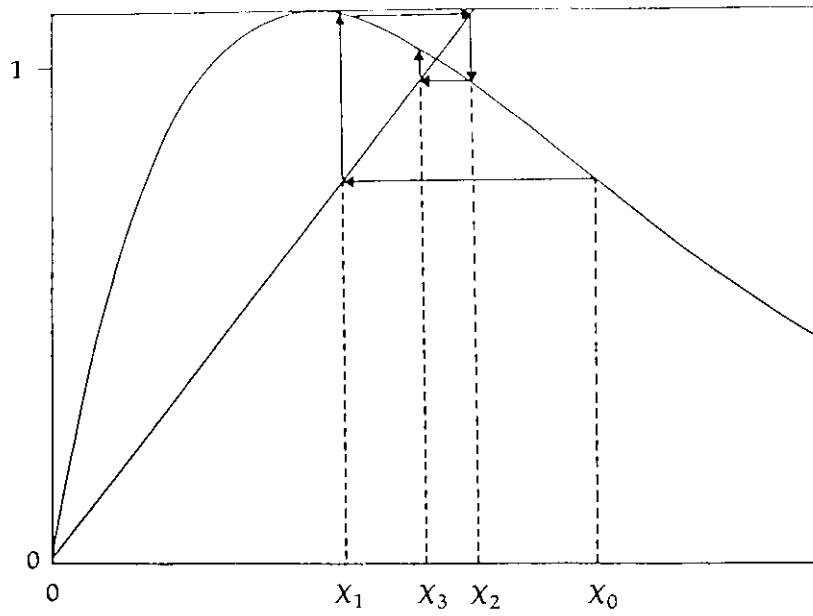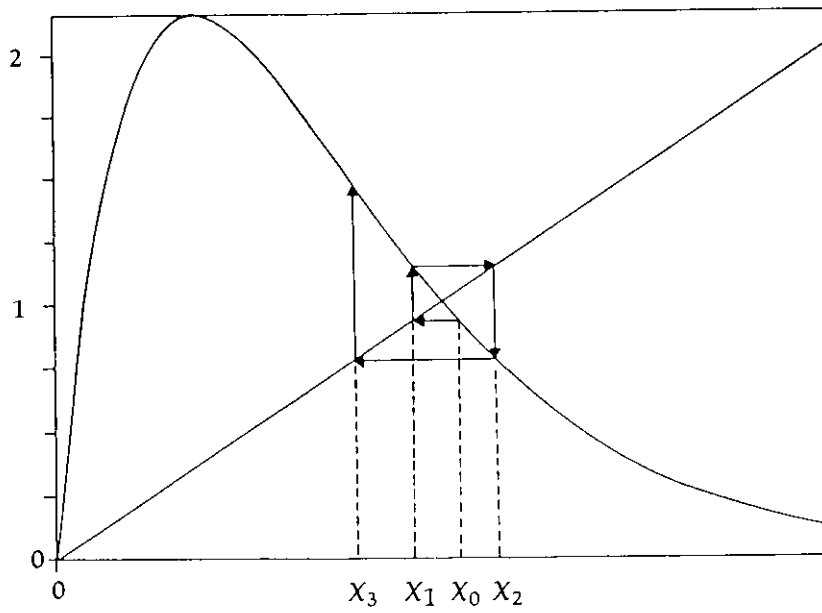
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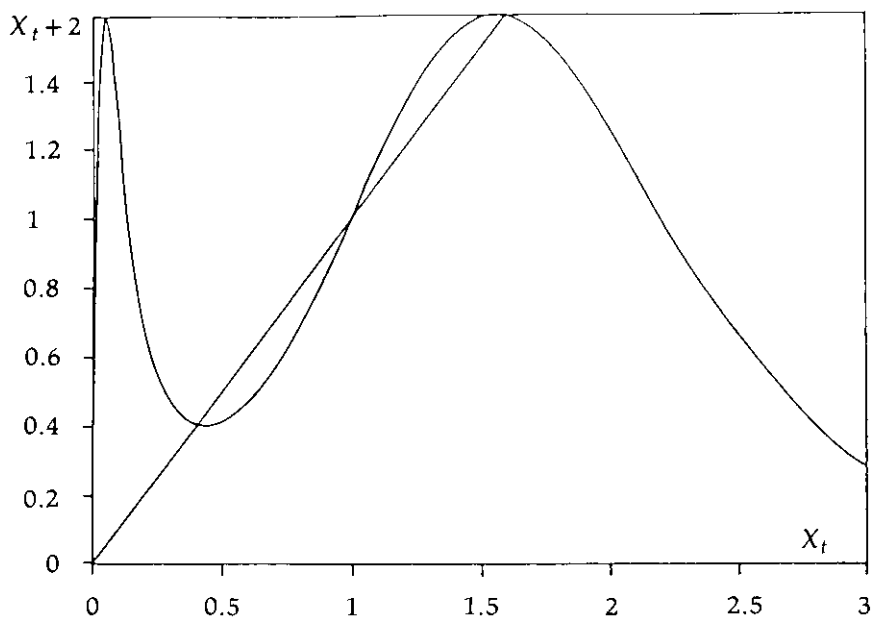Figure 3. The population graph for $|F'(1)| < 1$.



Figure 4. The population graph for $|F'(1)| > 1$.

Figure 5. The graph of $X_{t+2}$ vs. $X_t$.

**Exercises 9.** Show that

$$F^{(2)}(x) = x \, e^{r(2-x-xe^{r(1-x)})}.$$

10. Show that an equilibrium of period 2 occurs, that is, a point where $F^{(2)}(x) = x$, if

$$2 - x - xe^{r(1-x)} = 0. \tag{14}$$

11. Find one solution to Eq. (14) by inspection. (If you think about what we have shown so far, you should be able to guess the answer.)

The other two solutions of Eq. (14) may be found by numerical methods. Using Newton's Method for example, you will find that with $r = 2.3$, the other two solutions are $x_1 = .4078$ and $x_2 = 1.592$. These two solutions, known as *periodic points of period 2*, are important because they truly have period 2, whereas $x = 1$ has period 1.

Using the result of Exercise 3, we find that $F'(x_1) = .242$ and $F'(x_2) = -.682$ (using $x$ in place of N and letting $P = 1$). Since both of these are smaller in magnitude than 1, both points are stable. Together they form what is called a *limit cycle*. But as r gets bigger, $x_1$ and $x_2$ eventually succumb to the same fate as the original periodic point of period 1. When r becomes greater than 2.52, $x_1$ and $x_2$ become unstable and give rise to four stable periodic points of period 4.

The process, known as *bifurcation*, continues as r gets larger. The four periodic points of period 4 become unstable and bifurcate into eight periodic points of period 8, which become unstable and bifurcate into sixteen periodic points of period 16, and so forth. As r approaches a limiting value $r_c$, the bifurcations come faster and faster until finally, when $r > r_c$, the process becomes chaotic. In this region, there are an infinite number of periodic points, but these are usually unstable. It is important to realize that an unstable period will never be observed, since, if the population deviates even slightly from one of the periodic points, it will gradually drift farther away.

# 7. Computer Simulation

We can simulate the pattern of behavior described in the last section on a computer. The following BASIC program shows the change in population for any r over an arbitrary number of years:

```
10 INPUT "ENTER R, X, AND N: " ; R, X, N
20 FOR I = 1 TO N
30 PRINT I,X
40 X = X * EXP (R*(1 - X))
50 NEXT I
60 END
```

When you run this program, the computer will ask you to input values of R (the parameter of *r*), X (the initial population), and N (the number of years you want to observe).

If you are using a computer with a monitor rather than a printer, you will want to know how to stop and restart the computations. Otherwise, if N is large, you will see a blur of numbers disappear off the top of the screen. (On an Apple microcomputer, the printing may be stopped and restarted by holding the CONTROL key down and pressing S.)

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**Exercises 12.** Run the program with a value of R between 2.0 and 2.5. Let the initial population be any number between 0 and 3. You should see the population approach a limit cycle of period 2 within 20 years.

**13.** Try the program with the same R as in Exercise 12 but a different initial population. What happens? Can you explain this?

**14.** Run the program with R = 2.55. You should see a limit cycle with period 4.

**15.** Run the program with R = 2.7. Do you see any limit cycle? If you think you have found one, try making N really large (try 200) and see whether the pattern continues.

As you should have found in Exercise 14 and 15, $r_c$ is somewhere between 2.5 and 2.7. The correct value, up to four decimal places, is 2.6924. (To see how this may be calculated, see the article by May and Oster [8].)

**Exercise 16.** Run the program with R = 3.12 and N = 40. You should observe a limit cycle with period 3.

The cycle of period 3 you observed in Exercise 16 arises when r is large enough for there to be solutions of the equation $F(F(F(x)))$ = x other than x = 1.

**Exercise 17.** Show that this last equation holds if

$$3 - x[1 + e^{r(1-x)} + e^{r(2-x(1+e^{r(1-x)}))}] = 0. \tag{15}$$

In Fig. 6, we see the graph of the function found in Exercise 17 for r = 3.1024. This is the smallest value of r for which Eq. (15) has a solution other than x = 1. Once r becomes large enough, this cycle of period 3 also becomes unstable.

**Exercise 18.** Verify this last statement by running the program with R = 3.5.

Tien-Yien Li and James A. Yorke [7] have shown that if a model in Eq. (9) has a cycle of period 3, then it has cycles of period k for any positive integer k. Even if these cycles were stable, we would not be able to observe those with large periods unless we watched the population for a great number of years. In other words, a cycle that repeats every 1000 years is indistinguishable

from a random sequence of numbers if we observe the population for only 50 years.
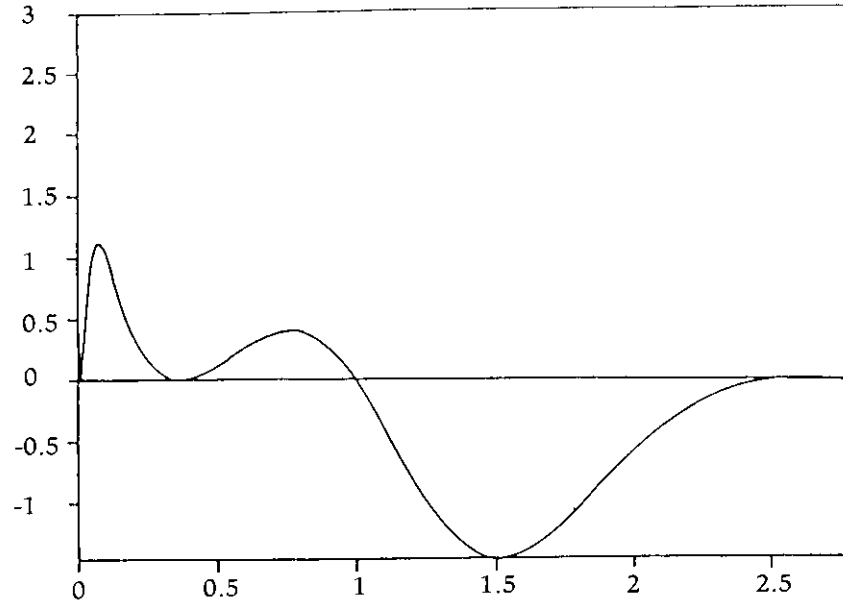


Figure 6. The graph of the left-hand side of Eq. (15)
as a function of $x$ for $r = 3.1024$.

The amazing thing is that such a simple model as Eq. (9) can exhibit such bizarre behavior. If you observed the data from Exercise 18 without knowing where it came from, you would be unlikely to guess the correct model. Perhaps even more amazing is that this behavior occurs for *any* model that has a hump-shaped graph as in Figure 1. You may wish to see the articles by Li and Yorke and by May and Oster for a more detailed explanation.

# 8. Dynamic Programming

For a variety of reasons, the strategy of catching the maximum sustainable yield is not necessarily best. Putting ourselves in the fishermen's waders, why do we want to keep the catch constant for all eternity if we won't be around long enough to fish it? Furthermore, might we be better off in the long run if we allow the catch to vary from one year to the next?

To pursue answers to those questions, imagine that we have a generation of salmon swimming around us, which we will

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designate generation 0. One action we can take is to catch none of them and let them spawn, hoping we will get a larger population next year. The opposite extreme is to catch them all right now. Or we can choose the intermediate action of catching a fraction of the population. Our goal is to maximize the total catch from generation 0 through generation $n$, when $n$ is some positive integer (perhaps the number of years we expect to be in business).

One way to tackle this problem is to use the technique of dynamic programming. Despite the formidable name, the reasoning behind dynamic programming is fairly simple. Suppose we have generation $i$ in front of us, where $0 \leq i \leq n$ and we decide to catch the fraction $u_i$ of $X_i$, where $0 \leq u_i \leq 1$. Such a $u_i$ is called the *exploitation rate*. After the catch, we only have

$$S_i = X_i(1 - u_i),  \tag{17}$$

the so-called spawning population, left to give birth to the next generation. Consequently, instead of Eq. (9), we now have

$$X_{i+1} = S_i e^{r(1 - S_i)}.  \tag{18}$$

For any $u_i$ chosen between 0 and 1, the catch is $u_i X_i$ (relative to the equilibrium population), and the next generation is $X_{i+1}$, as given by Eq. (18).

If we let $g(X_i)$ denote the maximum total catch from generations $i$ through $N$, given a generation $i$ population of $X_i$, we will get a maximum of $u_i X_i + g(X_{i+1})$ from generation $i$ through $N$ if we choose the exploitation rate $u_i$ right now. We therefore choose the $u_i$ that maximizes the quantity $u_i X_i + g(X_{i+1})$. In other words,

$$g(X_i) = \max_{0 \leq u_i \leq 1} \{ u_i X_i + g(X_{i+1}) \},  \tag{19}$$

with $X_{i+1}$ given by Eqs. (17) and (18).

The trick of dynamic programming is to use Eqs. (17), (18), and (19) to work backwards from the last generation to the current generation. If we are already at generation $n$, what is the best strategy? Making the assumption that we cannot profit from any fish left behind after this year, then we want to catch all the fish available, so $g(X_n) = X_n$. (Good for us, bad for any future generations of salmon lovers or fishermen.) For generation $n - 1$, using Eqs. (17), (18), and (19),

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$$g(X_{n-1}) = \max_{0 \le u_{n-1} \le 1} \quad u_{n-1} X_{n-1} + g(X_n)$$

$$= \max_{0 \le u_{n-1} \le 1} \quad u_{n-1} X_{n-1} + X_n \tag{20}$$

$$= \max_{0 \le u_{n-1} \le 1} \quad u_{n-1} X_{n-1} + S_{n-1} e^{r(1-S_{n-1})}$$

$$= \max_{0 \le u_{n-1} \le 1} \quad u_{n-1} X_{n-1} + X_{n-1}(1-u_{n-1}) e^{r(1-X_{n-1}(1-u_{n-1}))}$$

The usual way of getting $u_{n-1}$ from Eq. (20) is the discretization technique. Instead of regarding $u$ and $X$ as continuous variables, we regard them as discrete variables, taking on only a finite number of discrete values. For each possible $X_{n-1}$, we choose the $u_{n-1}$ which maximizes Eq. (20), using a computer to perform the calculations. Then we consider all the possible values of $X_{n-2}$. For each value, we choose $u_{n-2}$ to maximize Eq. (19) with $i = n - 1$.

We continue working our way backwards in this manner until we reach $X_0$. We know what $X_0$ is, and from the previous work we know what $u_0$ should be for this value of $X_0$. Then Eqs. (17) and (18) tell us $X_1$, and from the previous work we find the corresponding value of $u_1$. We continue to work forward until we reach generation $n$. To go into the details is beyond the scope of this unit, but interested readers may wish to investigate [14] and [15]. Let's just say that dynamic programming is an elegant and efficient (ef-fish-ient?) way to solve the problem.

**Exercise 19.** Suppose fishing regulations do not allow us to catch all the salmon in generation $n$, but instead require us to leave at least $L$ salmon behind, or, if $X_n$ is less than $L$, to leave behind all of $X_n$. Write a corresponding expression for $g(X_n)$.

Often next year's catch is more important to the fishing industry than the catch, say, ten years from now. For one thing, the distant future is too unpredictable. Another reason is that, if we catch more fish in the short term, the money we make from fishing could be invested elsewhere (perhaps in a Swiss bank account) to further increase our earnings. Thus, some biologists introduce a discount factor, $v$, into the catches, where $0 < v < 1$. The assumption is usually made that each year's catch is valued at a constant fraction $v$ of the previous year's catch. Then, instead of trying to

maximize the total catch

$$\sum_{i=0}^{n} u_i X_i,$$

we try to maximize the total discounted catch

$$\sum_{i=0}^{n} v^i u_i X_i.$$

**Exercises 20.** If $0 < v < 1$, prove that the sum

$$\sum_{i=0}^{n} v^i u_i X_i$$

puts more weight on the near future than the distant future.

**21.** Modify the dynamic programming formulation, Eq. (19), to maximize the total discounted catch.

# 9. Other Models

The Ricker model is not the only model used to study salmon. For example, another one developed by Beverton and Holt [2] yields the equation

$$N_{t+1} = \frac{1}{a + b/N_t} . \tag{21}$$

The articles by May and Oster [8] and by Lamberson and Biles [6] list related models.
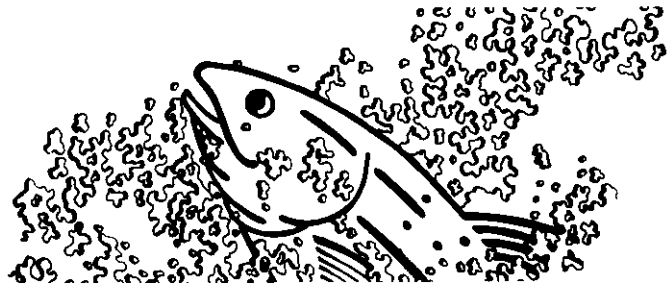
# 10. References

In addition to the books and articles referred to in the text, we have included a few other references [4, 5, 9, 10] that may be of interest.

1. Alexander, John W., *Curve Fitting via the Criterion of Least Squares*, UMAP Unit 321.

2. Beverton, R. J. H. and Holt, S. J., "On the dynamics of exploited fish populations," *Fishery Investigation of the Ministry of Agriculture Fisheries and Food* (Great Britain), Series II, Vol. 19 (1957), pp. 1-533.

3. Fisher, M. E., Goh, B. S. and Vincent, T. L., "Some stability conditions for discrete-time single species models," *Bulletin of Mathematical Biology*, Vol. 41 (1979), pp. 861-875.

4. Greenwell, Raymond N., "Whales and krill: a Mathematical model," *The UMAP Journal*, Vol. 3 (1982), pp. 165-183. Also published as UMAP Unit 610. This module develops a mathematical model for another ecological process and makes additional references to books and articles on mathematical ecology.

5. Jones, J. W., *The Salmon*, Harper and Brothers, 1959. This book, [9], and [10] provide a great deal of information on the life and times of salmon.

6. Lamberson, Roland, and Biles, Charles, "Polynomial models of biological growth," *The UMAP Journal*, Vol. 2, No. 2 (1981), pp. 9-25.

7. Li, Tien-Yien and Yorke, James A., "Period Three Implies Chaos," *American Mathematical Monthly*, Vol. 82 (1975), pp. 985-992.

8. May, Robert M. and Oster, George F., "Bifurcations and dynamic complexity in simple ecological models," *The American Naturalist*, Vol. 110 (1976), pp. 573-599.

9. Mills, Derek, *Salmon and Trout: a Resource, its Ecology, Conservation and Management*, St. Martin's Press, 1971.

10. Netboy, Anthony, *The Salmon: Their Fight for Survival*, Houghton Mifflin Company, 1974.

11. Ricker, W. E., "Stock and Recruitment," *Journal of the Fisheries Research Board of Canada*, Vol. 11 (1957), pp. 559-623.

12. Shepard, M. P. and Withler, F. C., "Spawning stock size and resultant production for Skeena sockeye," *Journal of the Fisheries Research Board of Canada*, Vol. 15 (1958), pp. 1007-1025.

13. Thomas, William P., Pomerantz, Mark J. and Gilpin, Michael E., "Chaos, asymmetric growth and group selection for dynamic stability," *Ecology*, Vol. 61 (1980), pp. 1312-1320.

14. Walters, Carl J., "Optimal harvest strategies for salmon in relation to environmental variability and uncertain production parameters," *Journal of the Fisheries Research Board of Canada*, Vol. 32 (1975), pp. 1777-1784.

15. Walters, Carl J., "Optimum escapements in the face of alternative recruitment hypotheses," *Canadian Journal of Fisheries and Aquatic Sciences*, Vol. 36 (1981), pp. 678-689.

# 11. Answers to Exercises

1. $N_{t+1} = kN_t$, so $N_1 = kN_0$, $N_2 = kN_1 = k^2N_0$, $N_3 = kN_2 = k^3N_0$, and, in general, $N_t = N_0k^t$. Mathematical induction could be used to make this more rigorous.

2. $\dfrac{dR}{dt} = -CR$.

Separating variables and integrating both sides, we have

$$\frac{dR}{dt} = -C\,dt,\ ln\,R = -Ct + K,\ R = e^{-Ct}e^K.$$

When $t = 0$, $R = e^K$, so we denote $e^K$ by $R_0$. Thus $R = R_0\,e^{-Ct}$.

3. $f'(N) = e^{r(1-N/P)} + N e^{r(1-N/P)}(-r/P) = (1-r N/P) e^{r(1-N/P)}$.

4. $\lim\limits_{N \to \infty} N e^{r(1-N/P)} = \lim\limits_{N \to \infty} \dfrac{e^{r}N}{e^{r N/P}}$ .

   Since the numerator and denominator approach $\infty$, we invoke L'Hopital's rule, yielding

   $$\lim\limits_{N \to \infty} \dfrac{e^{r}}{e^{r N/P} \cdot (r/P)} = 0$$

5. To maximize $F(N) - N$, set the derivative equal to 0:
   $f'(N) - 1 = 0$ or $f'(N) = 1$.

6. Since $F'(N^*) = 1$, the answer to Exercise 3 tells us that

   $$(1 - rN^*/P)\, e^{r(1-N^*/P)} = 1,$$

   $$e^{r(1-N^*/P)} = 1/(1 - rN^*/P).$$

   The maximum sustainable yield is

   $$f(N^*) - N^* = N^* e^{r(1-N^*/P)} - N^* = N^*\left(\dfrac{1}{1 - rN^*/P} - 1\right)$$

7. $N_{t+1}/N_t = e^{r(1-N_t/P)}$,
   so $y_t = ln(N_{t+1}/N_t)$
   $= r(1 - N_t/P)$
   $= r - N_t r/P$,

   which is the equation of a line with slope $-r/P$ and $y$-intercept $r$.

8. $F'(X) = (1 - rN)\, e^{r(1-N)}$. Since $P = 1$,

   $$|F'(P)| < 1, \ |1-r| < 1, 0 < r < 2.$$

   We have already assumed $r > 0$, so we only need $r < 2$.

9. $F^{(2)}(X) = F(F(X))$
   $= F(X)\, e^{r(1-F(X))}$
   $= xe^{r(1-x)}e^{r(1 - Xe^{r(1-x)})}$
   $= xe^{r(1-x+1-xe^{r(1-x)})}$
   $= xe^{r(2-x-xe^{r(1-x)})}$.

**10.** If $x = F^{(2)}(x) = xe^{r(2-x-xe^{r(1-x)})}$ , then
$e^{r(2-x-xe^{r(1-x)})} = 1$, so $2 - x - xe^{r(1-x)} = 0$.

**11.** $x = 1$ is a solution.

**12.** The limit cycle depends on the value of $r$ chosen. If $r = 2.2$, a limit cycle consisting of the two points .49706 and 1.50294 is seen by the time $N = 20$.

**13.** Since the periodic points are globally stable, we should see the same limit cycle regardless of the starting point.

**14.** The cycle consists of the four points .22037, 1.60900, .34050, 1.83012.

**15.** There is no stable limit cycle. Any one that seems to appear will drift if $N$ gets large enough.

**16.** The limit cycle consists of the three points .01458, .3155, and 2.670.

**17.** Using the result of Exercise 10,

$$F^{(3)}(x) = F(F^{(2)}(x)) = F^{(2)}(x)\, e^{r(1-F^{(2)}(x))}$$
$$= xe^{r(2-x-xe^{r(1-x)})}e^{r(1-xe^{r(2x-xe^{r(1-x)})})}$$
$$= xe^{r(2-x-xe^{r(1-x)}\,+1-xe^{r(2-x-xe^{r(1-x)})})}$$
$$= xe^{r(3-x-xe^{r(1-x)}-xe^{r(2-x-xe^{r(1-x)})})}.$$

This is equal to $x$ if $3 - x - xe^{r(1-x)} - xe^{r(2-x-xe^{r(1-x)})} = 0$, or $3 - x(1 + e^{r(1-x)} + e^{r(2-x-xe^{r(1-x)})}) = 0$.

**18.** There is no stable limit cycle. The points appear to be random.

**19.** $g(X_n) = \max\{X_n - L, 0\}$.

**20.** If $m < n$, then $v^m > v^n$ since $0 < v < 1$.

**21.** $g(X_i) = \max\{u_i X_i + vg(X_i + 1)\}$.
$\qquad\quad 0 \le u_i \le 1$