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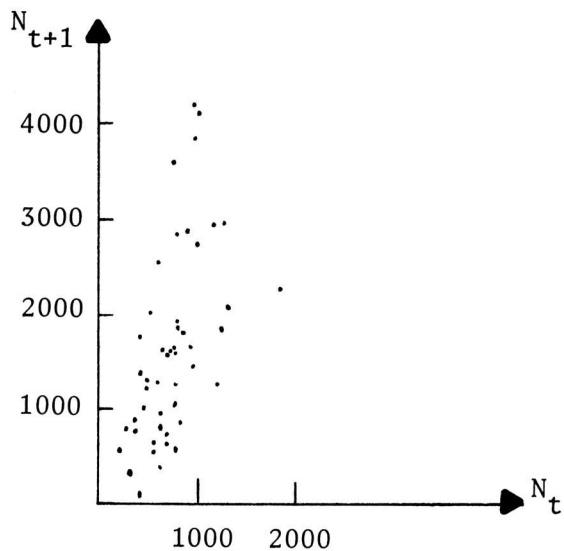
UNIT 653

MODULES AND MONOGRAPHS IN UNDERGRADUATE
MATHEMATICS AND ITS APPLICATIONS PROJECT

The Ricker Salmon Model

by

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Applications to Environmental Science

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Intermodular Description Sheet: UNIT 653**Title:** The Ricker Salmon Model**Author:** Raymond N. Greenwell
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Albion, Michigan 49224**Math Field:** Difference equations**Application Field:** Ecology**Target Audience:** Students in a differential equations or modelling 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 is to develop, through a community of users and developers, a system of instructional modules in undergraduate mathematics and its applications that may be used to supplement existing courses and from which complete courses may eventually be built.

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The Ricker Salmon Model

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 ex-salmon 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 birth-place. 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.

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

$$N_{t+1} \propto N_t, \quad (1)$$

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 rate proportional to their number. If we let R be the population of the new generation, known as recruits, then

$$\frac{dR}{dt} = -cR, \quad (2)$$

where c is a constant of 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

$$R = R_0 e^{-ct}, \quad (3)$$

where R_0 is the initial recruit population.

Exercise 2. Derive Eq. (3).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Exercise 4. Show that $\lim_{N \rightarrow \infty} f(N) = 0$.

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.

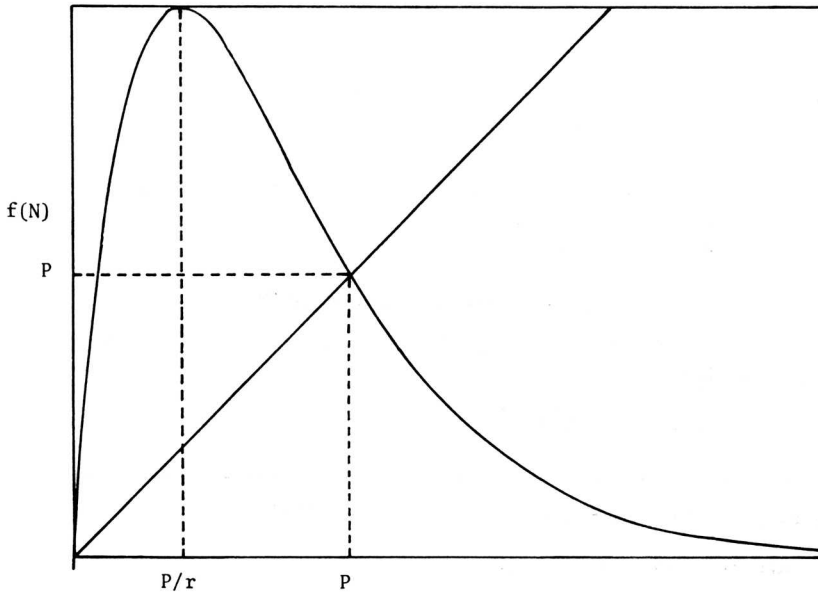


Figure 1. The graph of $F(N)$ (population of the next generation) vs. N (population of this generation).

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. Figure 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.

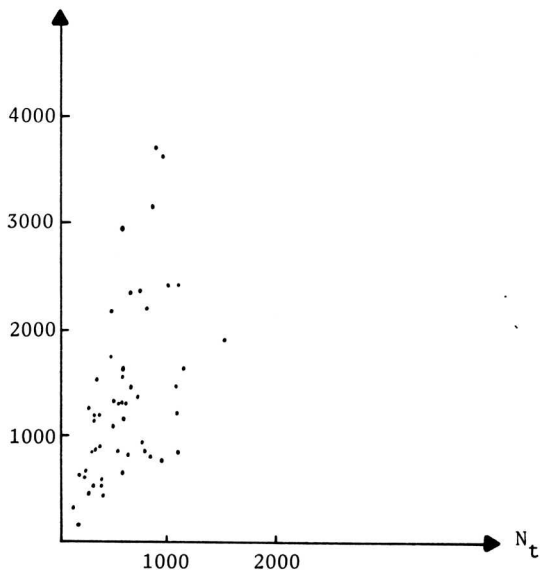


Figure 2. The plot of N_{t+1} vs. N_t for data taken from [12]

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:

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

where σ_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 θ -Ricker model:

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

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 θ 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., θ 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, \dots, N_n , is to introduce a new variable $y_t = \ln(N_{t+1}/N_t)$ and plot y_t vs. N_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. Mathematically, this says

$$|X_{t+1} - P| \leq |X_t - P| \quad (12)$$

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

$$\left| \frac{F(X_t) - F(P)}{X_t - P} \right| \leq 1 \quad (13)$$

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 inequality 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 and 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 $F^{(2)}(X)$.

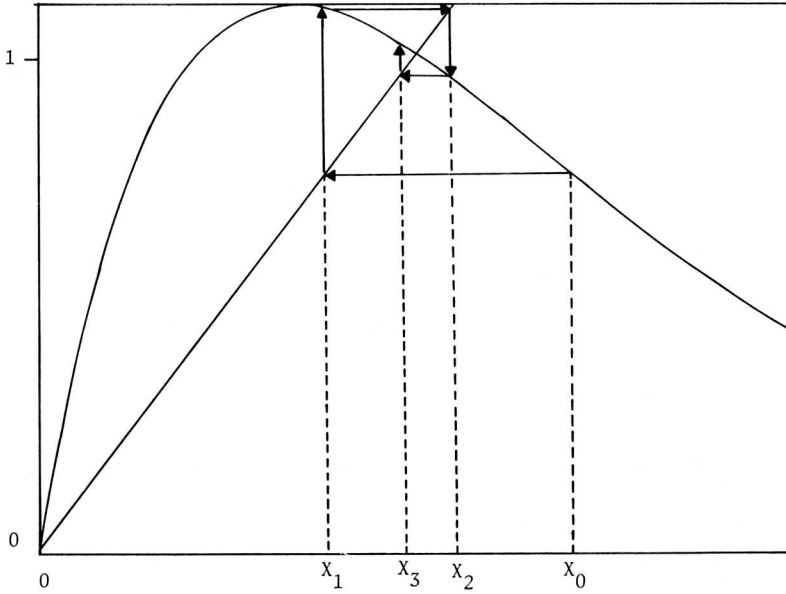


Figure 3. The population graph for $|F'(1)| < 1$.

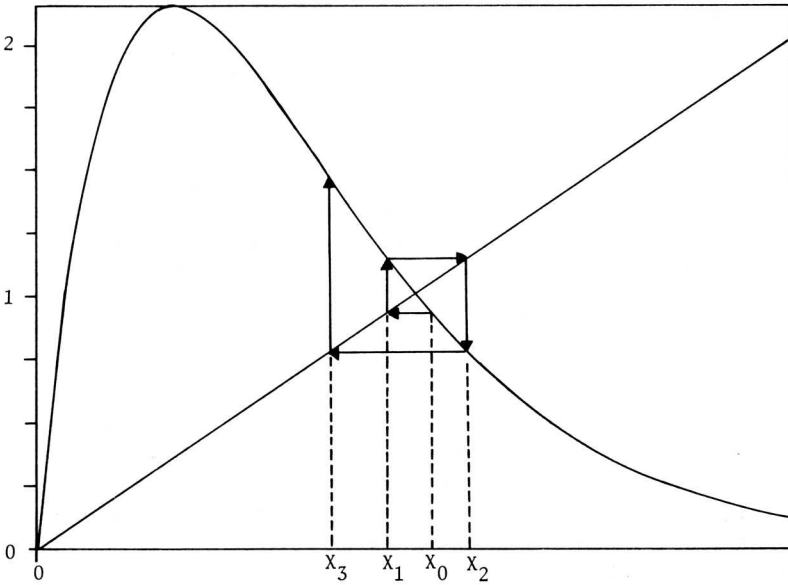


Figure 4. The population graph for $|F'(1)| > 1$.

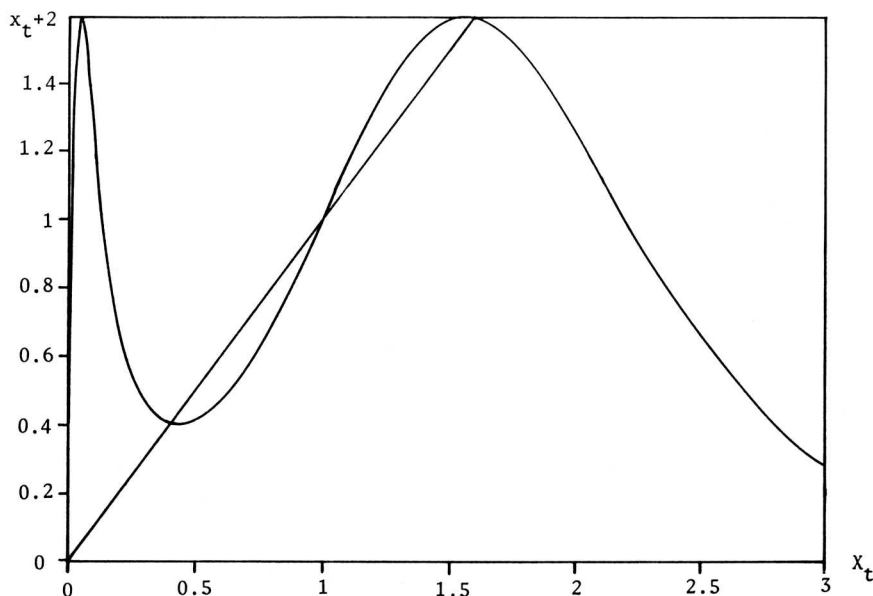


Figure 5. The graph of X_{t+2} vs. X_t .

Exercise 9. Show that

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

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

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

Exercise 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 further 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 r), X (the initial population), and N (the number of years you want to observe).

If you are using a computer with 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.)

Exercise 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.

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

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

Exercise 15. Run the program with $R = 2.7$. Do you see any limit cycle? If you think you have found one, try making R 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

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

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

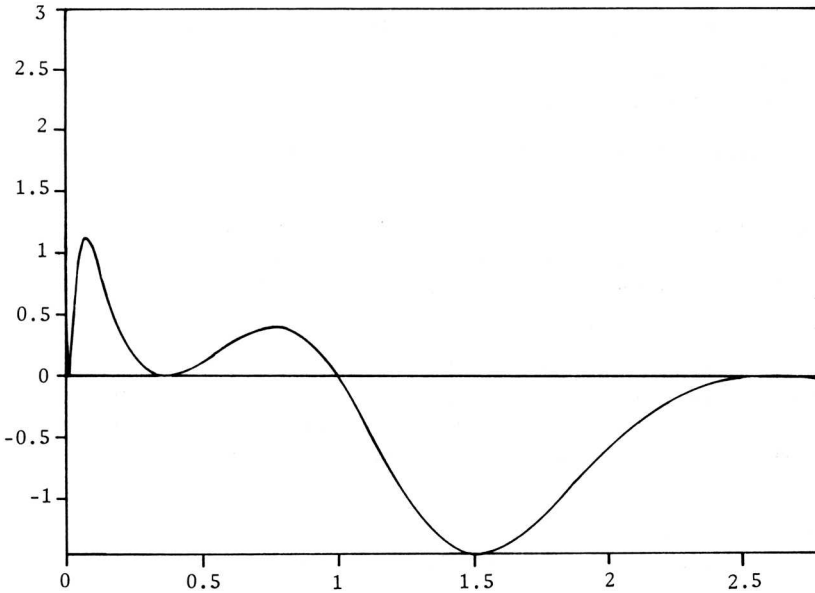


Figure 6. The graph of the left-hand side of Eq. (15) as a function of x for $r = 3.1024$.

repeats every 1000 years is indistinguishable from a random sequence of numbers if we observe the population for only 50 years.

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 designate generation 0. One action we can take is to

