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**ABSTRACT**  
 This is one in a series of SMSG supplementary and enrichment pamphlets for high school students. This series is designed to make material for the study of topics of special interest to students readily accessible in classroom quantity. Topics covered include the simplest version of the growth of a single population, a more realistic model of one population, and one species preying on another. (MP)

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**SCHOOL  
MATHEMATICS  
STUDY GROUP**

**SP-26**

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**SUPPLEMENTARY and  
ENRICHMENT SERIES**

**THE MATHEMATICAL THEORY  
OF THE STRUGGLE FOR LIFE**

Edited by M. Philbrick Bridgess

U.S. DEPARTMENT OF HEALTH  
EDUCATION & WELFARE  
NATIONAL INSTITUTE OF  
EDUCATION

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## PREFACE

Mathematics is such a vast and rapidly expanding field of study that there are inevitably many important and fascinating aspects of the subject which, though within the grasp of secondary school students, do not find a place in the curriculum simply because of a lack of time.

Many classes and individual students, however, may find time to pursue mathematical topics of special interest to them. This series of pamphlets, whose production is sponsored by the School Mathematics Study Group, is designed to make material for such study readily accessible in classroom quantity.

Some of the pamphlets deal with material found in the regular curriculum but in a more extensive or intensive manner or from a novel point of view. Others deal with topics not usually found at all in the standard curriculum. It is hoped that these pamphlets will find use in classrooms in at least two ways. Some of the pamphlets produced could be used to extend the work done by a class with a regular textbook but others could be used profitably when teachers want to experiment with a treatment of a topic different from the treatment in the regular text of the class. In all cases, the pamphlets are designed to promote the enjoyment of studying mathematics.

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## FOREWORD

This pamphlet introduces the pupil to the notion of a mathematical model by which the solution of an actual problem can be attempted. It shows how one can start with a very simple case, which may not be very realistic, and change the conditions to approach those which do exist.

By way of preparation, the pupil should be familiar with quadratic equations, geometric progressions and inequalities. The number of proofs is limited. The computation is not very difficult, and, except for two examples, is not extensive. In the two examples, the pupil sees how the changing conditions gradually bring about a reversal of a situation, namely, the number of two kinds of fish which can survive when one fish is the food of the other.

## CONTENTS

Section	Page
1. Introduction . . . . .	1
2. Growth of a Single Population, Simplest Version . . . . .	1
3. The Simplest Version, Continued . . . . .	3
4. One Population, More Realistic Model . . . . .	6
5. One Species Preying on Another . . . . .	10
6. Summary and Some Extensions . . . . .	12
BIBLIOGRAPHY . . . . .	17
ANSWERS . . . . .	18

## THE MATHEMATICAL THEORY OF THE STRUGGLE FOR LIFE

### 1. Introduction

During World War I, the Italians were unable to send their fishing fleets into the Adriatic since their enemy was nearby. After the war, the Italians resumed fishing on a large scale. They were amazed to find that there were fewer fish of the kind that they had been catching than there had been before. They expected, of course, that since they had not been catching these fish for four years, that there would be many more of them.

The leaders of the Italian fish industry came to Professor Vito Volterra, one of the greatest Italian mathematicians, and asked him if he could give an explanation. He worked out a mathematical theory of the "Struggle for Life". In this pamphlet, we shall try to explain some of his main ideas in terms of high school algebra. Additional material on the topic is given in the bibliography at the end of the pamphlet.

### 2. Growth of a Single Population, Simplest Version

Let us consider a population of bacteria in a culture dish or in your blood stream. Suppose that we determine the population every day by some method or other which will give us a reasonably accurate number. We shall use the expression "to count the population" but we are not going to actually count 1,000,000 bacteria. We are reasonably certain that the number of bacteria will depend upon the length of time that our experiment has been in progress.

In the same way that you have used, say,  $f(x) = x + 2$  and found that  $f(3) = 3 + 2$ , we are going to let  $t$  be the number of days since we began the experiment and  $x(t)$  be the population on the  $t$ -th day.  $x(0)$  is the initial population,  $x(1)$  is the population after 1 day, and so on.

Suppose that we obtain the following results:

<u>t</u>	<u>x(t)</u>	<u>change in population</u>
0	1,000,000	10,000
1	1,010,000	10,100
2	1,020,100	
3	1,030,301	
4	1,040,604	
5	1,051,010	

Table 1.

The change in population during the first day is the population at the end of one day minus the population at the start, that is,  $x(1) - x(0)$ . Thus, we find that the change during the first day is

$$x(1) - x(0) = 1,010,000 - 1,000,000 = 10,000.$$

Similarly, the change during the second day is

$$x(2) - x(1) = 1,020,100 - 1,010,000 = 10,100.$$

The first example of Problem Set 1 is to complete the table.

During each day any particular bacterium has a certain chance of reproducing and a certain chance of dying. Say that the chance, or probability, of reproducing during the period of 1 day is .03. That is, suppose that, on the average, 3 bacteria out of 100 reproduce during 1 day. Suppose also that the chance of any particular bacterium dying during this period is .02. Then the excess of births over deaths is 1 out of 100 per day. In other words, the relative rate of growth is .01 per day.

We can state this result in the following way. The relative rate of growth during the first day is the ratio of the change in population to the whole population. In our example, this would be:

$$\frac{x(1) - x(0)}{x(0)} = \frac{1,010,000 - 1,000,000}{1,000,000}$$

### Problem Set 1

1. Copy Table 1 and leave space on the right for an additional heading. Complete the column in Table 1 entitled "Change in Population".
2. Label the space on the right "Relative Rate of Growth". Compute the relative rate of growth of the population for each day. Carry out your computation to 2 decimal places. What do you notice?



3. Assume that the relative rate of growth remains constant. Predict the value of  $x(6)$ .
4. Solve the equation  $\frac{x(7) - x(6)}{x(6)} = .01$  for  $x(7)$  as the unknown.
5. Solve the equation  $\frac{x(t+1) - x(t)}{x(t)} = r$  for  $x(t)$  as the unknown.

### 3. The Simplest Version, Continued

As a first approach, on the basis of a great deal of experimentation, we shall assume that the relative rate of growth of the population is a constant. If this constant is .01, then we obtain the following equations:

$$\frac{x(1) - x(0)}{x(0)} = .01$$

$$\frac{x(2) - x(1)}{x(1)} = .01$$

$$\frac{x(3) - x(2)}{x(2)} = .01$$

and, in general,

$$\frac{x(t+1) - x(t)}{x(t)} = .01$$

### Problem Set 2

1. Solve the first of the above equations for  $x(1)$  in terms of  $x(0)$ , the second for  $x(2)$  in terms of  $x(1)$ , the third for  $x(3)$  in terms of  $x(2)$ , and, in the general case, for  $x(t+1)$  in terms of  $x(t)$ .
2. Obtain an expression for  $x(2)$  in terms of  $x(0)$ .
3. Similarly, find expressions for  $x(3)$ ,  $x(4)$ , and  $x(5)$  in terms of  $x(0)$ .
4. Suggest a formula for  $x(t)$  in terms of  $x(0)$ .
5. If  $a$  is the first term of a geometric progression and  $r$  is the common ratio;
  - (a) What is the formula for the  $n^{\text{th}}$  term?
  - (b) What is the formula for the  $(n+1)^{\text{st}}$  term?
  - (c) Which term is  $x(5)$  if  $x(0)$  is the first term?
  - (d) Which term is  $x(t)$  if  $x(0)$  is the first term?

Our next step is to solve our problem about bacteria for any relative rate of growth. Let us assume that this rate of growth is a constant,  $r$ . Then we have the equations:

$$\frac{x(1) - x(0)}{x(0)} = r$$

or

$$x(1) - x(0) = rx(0)$$

$$x(2) - x(1) = rx(1), \dots$$

$$x(t + 1) - x(t) = rx(t)$$

### Problem Set 3

1. Solve the first of the above equations for  $x(1)$  in terms of  $r$  and  $x(0)$ , for the second for  $x(2)$  in terms of  $r$  and  $x(1)$ , and, in the general case, for  $x(t + 1)$  in terms of  $r$  and  $x(t)$ .
2. Obtain an expression for  $x(2)$  in terms of  $r$  and  $x(0)$ .
3. If  $x(3) = (1 + r)x(2)$ , obtain an expression for  $x(3)$  in terms of  $r$  and  $x(0)$ .
4. Suggest a formula for  $x(t)$  in terms of  $r$  and  $x(0)$ .
5. What is the formula for finding the amount of money,  $A$ , if  $P$  dollars is put in the bank and left to be compounded annually for  $n$  years at  $r$  per cent?
6. Compare your results in Exercise 4 and Exercise 5.

So far we have imagined that the population is counted every day. We can also consider what happens if we use a different time interval. Suppose that we count (estimate) the population every  $h$  days. The number  $h$  might be 7 (weekly observations),  $\frac{1}{24}$  (hourly observations), or any other number we choose. Let us assume that the relative change in population per unit time is a fixed number  $r$ .

Then our observations are made at the times:

$$t = 0, h, 2h, 3h, \dots, nh, \dots,$$

and the observed populations are

$$x(0), x(h), x(2h), x(3h), \dots, x(nh), \dots$$

The changes in population are

$$x(h) - x(0), \quad x(2h) - x(h), \quad \dots, \quad x((n+1)h) - x(nh)$$

and the relative changes are

$$\frac{x(h) - x(0)}{x(0)}, \quad \frac{x(2h) - x(h)}{x(h)}, \quad \text{etc.}$$

The relative rate of change is given by the formula:

$$\text{relative rate of change} = \frac{\text{relative change}}{\text{length of time interval}}$$

Thus, during the first time interval, the relative rate of change is:

$$\frac{x(h) - x(0)}{x(0)} + h = \frac{x(h) - x(0)}{hx(0)}$$

By our assumption, this must be equal to the given constant  $r$ :

$$r = \frac{x(h) - x(0)}{hx(0)}$$

and we obtain

$$x(h) - x(0) = rhx(0)$$

#### Problem Set 4

1. Write the equations for each of the other time intervals:  $x(2h)$ ,  $x(3h)$ ,  $x(nh)$ , and  $x((n+1)h)$ .
2. Solve these equations to express  $x(h)$  in terms of  $x(0)$ ,  $x(2h)$  in terms of  $x(h)$ , ..., and  $x((n+1)h)$  in terms of  $x(nh)$ .
3. Find  $x(h)$ ,  $x(2h)$ , ...,  $x(nh)$  in terms of  $x(0)$ .
4. Remember that  $t = nh$  and show how the last equation of Exercise 3 can be written as  $x(t) = c^t x(0)$ .
5. Give a formula for the constant  $c$  in terms of  $r$  and  $h$ .
6. Compare the results in Exercise 4 and Exercise 5 with the compound interest formulas for cases in which the period of compounding is semi-annually and quarterly.

7. Make a table of the values of  $C$  for various values of  $r$  and  $h$ .

$\underline{r}$	$\underline{h}$	$\underline{C}$	$\underline{r}$	$\underline{h}$	$\underline{C}$	$\underline{r}$	$\underline{h}$	$\underline{C}$
1	1	2	.5	1		2	1	
1	.5		.5	.5		2	.5	
1	.1		.5	.1		2	.1	
1	.01		.5	.01		2	.01	
1	.001		.5	.001		2	.001	

8. Let  $C(r,h)$  be the value of  $C$  for given values of  $r$  and  $h$ . Compute  $C(1,.001)^2$  and compare with  $C(2,.001)$ ;  $C(.5,.001)^2$  and compare with  $C(1,.001)$ .

9. Prove the inequalities:

(a) If  $r > 0$ , then  $(1 + r)^2 > 1 + 2r$

(b) If  $r > 0$ , and  $(1 + r)^n > 1 + nr$ , then  $(1 + r)^{n+1} > 1 + (n + 1)r$

(c)  $(1.000001)^{1,000,000,000} > 1.001$

(d) Find a number  $n$  such that  $(1.000001)^n > 1,000,000$

#### 4. One Population, More Realistic Model

As you can see from Problem Set 4, if a population grows according to the law of the previous section, then it ultimately becomes larger than any number you may choose. This is not very plausible. For a bacterial population in an agar dish or in a man's blood stream is strictly limited in size. There is just not room enough for more than so many, and besides, they would be using up their food supply and be poisoning their environment (as well as the man!) with their waste products.

We say that the mathematical model, or mental picture, of the growth of the population is not realistic enough. As in most other problems in which we try to apply mathematics to the real world, we find that the real world is too complicated for our poor feeble human minds to grasp. Hence, we try to idealize and simplify the actual situation until we obtain something easy enough for us to handle. We try to pick out the most important features of the real problem and incorporate them into a mathematical model. We often start

out with a very simple mathematical model. After we have studied it thoroughly and understand this first approximation to the real world, we then, step by step, introduce new ideas to make our model more realistic.

This is what we shall do now. Our previous model assumed a certain basic relative rate of excess of births over deaths, and that this basic rate is constant. As a first attempt to improve this, let us assume a correction which takes into account the rate at which the population uses up its food supply and poisons its environment. Let us assume that this correction is proportional to the size of the population.

We can express our assumption in mathematical language like this. Before, we assumed that  $r$ , the relative rate of change of the population, is constant. Now we are assuming that  $r$  depends on the size,  $x$ , of the population:

$$r = R - cx.$$

Here  $R$  is the basic rate of excess of births over deaths, and  $cx$  is a correction proportional to the size of the population. We assume that  $R$  and  $c$  are positive constants.

If we observe the population every  $h$  days, then the equation expressing the relation between the population  $x(t)$  and  $x(t + h)$  at successive observations is

$$\frac{x(t + h) - x(t)}{hx(t)} = R - cx(t).$$

If we solve this equation for  $x(t + h)$  as the unknown, then we can predict the population  $h$  days from now provided that we know the population now (at time  $t$ ).

### Problem Set 5

1. Solve the equation for  $x(t + h)$  and put your result in the form

$$x(t + h) = ( \quad ) x(t) - ( \quad ) (x(t))^2$$

2. Let  $R = .01$ ,  $h = 1$ ,  $c = .000001$  and  $x(0) = 1,000,000$ . Make a table showing the population at various times.

$t$	$x(t)$
0	1,000,000
1	
2	
3	
4	
5	

3. Work out tables for the following cases for  $t = 1$ ,  $t = 2$ .

$\frac{R}{c}$	$h$	$c$	$x(0)$
.01	1	.000001	1,000,100
.01	1	.000001	900,000
.01	.5	.000001	1,000,100
.01	.01	.000001	1,000,100

4. What is the significance of  $x = \frac{R}{c}$ ?

You have obtained an equation of the form:

$$x(t + h) = a x(t) - b(x(t))^2 \quad (1)$$

for predicting the population at the time  $t + h$  in terms of the population at the time  $t$ . The values of  $a$  and  $b$  were found in Exercise 1 of Problem Set 5.

We can give a graphical process for finding the prediction. First we draw the graph of the equation

$$y = ax - bx^2 \quad (2)$$

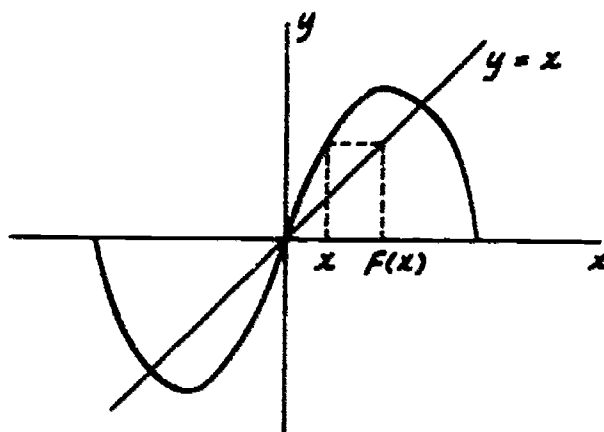
( $y$  is  $x(t + h)$  and  $x$  is  $x(t)$  in Equation (1)). You recognize this curve as one of the family of parabolas.

Now if you have the graph of an equation, it is easy to calculate  $y$  from  $x$  graphically.

We shall illustrate a method, which can be used, with an equation somewhat different from ours. Let us use:

$$y = 4x - \frac{x^3}{4} = F(x)$$

The combined graph of our illustrative equation and  $y = x$  looks like this:



Now if  $x$  is given, we locate the corresponding point on the  $x$ -axis, go vertically to the curve  $y = 4x - \frac{x^3}{4}$ , then horizontally across to the line  $y = x$ , then vertically down to the  $x$ -axis again. This new point on the  $x$ -axis will represent the number  $4x - \frac{x^3}{4}$ .

If you apply this process to the graph of

$$x(t+h) = a x(t) - b(x(t))^2$$

$$(y = ax - bx^2)$$

and start with  $x = x(0)$ , the initial population, you will obtain  $x(h)$ , the population  $h$  days later. If you repeat the process, using  $x(h)$  now, you will obtain  $x(2h)$ . If you iterate the process, you will obtain successively  $x(3h)$ ,  $x(4h)$ , etc.

#### Problem Set 6

1. For what values of  $x(t)$  is it true that  $x(t+h) = x(t)$ ? Give the biological and the graphical interpretation.
2. Let  $E$  be the non-zero solution of the previous problem. If  $x(0) < E$ , is  $x(h) > x(0)$  or is  $x(h) < x(0)$ ? What happens if you iterate the process? How does  $x(t)$  behave for large  $t$ ?
3. If  $x(0) = \frac{1}{b}$ , what is  $x(h)$ ? What happens from then on? (See Problem Set 5, Exercise 1 for the value of  $b$ .)
4. If  $\frac{1}{b} < x(0) < \frac{a}{b}$ , what can you say about  $x(h)$ ? What happens from then on? (See Problem Set 5, Exercise 1 for the value of  $a$ .)
5. If  $x(0) > \frac{a}{b}$ , what can you say about  $x(h)$ ? What is the biological interpretation? Can you suggest any limitation of our model? How might it be improved?
6. Let  $z(t) = E - x(t)$  be the deviation of the population from equilibrium at the time  $t$ . Show that  $z(t+h)$  is related to  $z(t)$  by an equation of the form:

$$z(t+h) = A z(t) + B (z(t))^2$$

where  $A$  and  $B$  are constant. Find formulas for  $A$  and  $B$  in terms of  $R$ ,  $h$ , and  $c$ . Show that if  $R$  and  $c$  are given, then  $A > 0$  for all sufficiently small values of  $h$ .

7. Show that if  $|z(t)| < \frac{1-A}{B}$ , then  $|z(t+h)| < |z(t)|$ .

## 5. One Species Preying on Another

Imagine now that we have a lake containing minnows and pike, and that the minnows are part of the food supply for the pike. We assume that these populations are observed every  $h$  days, and we denote the populations of minnows and pike at the time  $t$  by  $x(t)$  and  $y(t)$  respectively. As before, we express the laws governing the changes of these populations in terms of the relative rates of change

$$r_x = \frac{x(t+h) - x(t)}{h x(t)}, \quad r_y = \frac{y(t+h) - y(t)}{h y(t)}$$

Let us examine  $r_x$  at a time when the populations are  $x$  and  $y$ , respectively. We assume that there is a certain basic rate of excess of births over deaths for the minnows, given by a positive constant  $a$ . There is a correction for the size of the minnow population, which uses up its food supply and poisons its environment, and we assume that this correction is proportional to  $x$ . This correction contributes a term  $-bx$ , where  $b$  is a positive constant. Furthermore, the more pike there are, the more they eat the minnows. If we assume a constant rate of consumption of minnows per pike per day, this gives us a correction of the form  $-cy$ , where  $c$  is a positive constant. We thus arrive at the equation

$$r_x = a - bx - cy, \tag{1}$$

expressing the relative rate of growth of the minnow population when the minnow and pike populations are  $x$  and  $y$ , respectively.

Reasoning in the same way, we arrive at the equation

$$r_y = A + Bx - Cy \tag{2}$$

where  $A$ ,  $B$ , and  $C$  are positive constants. Notice that the more minnows there are, the more food there is per pike, and the better it is for the pike. This explains the term  $Bx$ , with a positive coefficient.

We can then set up the equations describing how the populations change from the time  $t$  to the time  $t+h$ :

$$\frac{x(t+h) - x(t)}{h x(t)} = a - b x(t) - c y(t), \tag{3}$$

$$\frac{y(t+h) - y(t)}{h y(t)} = A + B x(t) - C y(t). \tag{4}$$

In Problem Set 7 you will solve these two equations for  $x(t+h)$  and  $y(t+h)$  as unknowns.



We can now do some numerical experiments. We can assume numerical values for the coefficients  $a$ ,  $b$ ,  $c$ ,  $A$ ,  $B$ ,  $C$ , and the time interval  $h$ . We can then see what happens if we start out with different initial states  $x(0)$ ,  $y(0)$ . We can represent a state of the populations by means of a point  $(x,y)$  in the plane. This enables us to picture the various possibilities.

Problem Set 7

1. Solve Equations (3) and (4) for  $x(t + h)$  and  $y(t + h)$  and express your results in the form:

$$x(t + h) = x(t) \left( \underline{\hspace{1cm}} + \underline{\hspace{1cm}} x(t) + \underline{\hspace{1cm}} y(t) \right)$$

$$y(t + h) = y(t) \left( \underline{\hspace{1cm}} + \underline{\hspace{1cm}} x(t) + \underline{\hspace{1cm}} y(t) \right)$$

Warning! Some of the coefficients are negative.

2. Assume the following values

$$a = .05, \quad b = .000001, \quad c = .00002,$$

$$A = .01, \quad B = .00001, \quad C = .0001.$$

Take  $h = 1$ . Work out the changes in the populations if the initial populations are  $x_0 = 16,000$  and  $y_0 = 2000$ . Tabulate your results like this

t	x	y
0	16,000	2,000
1		
2		
3		
4		
5		

Carry out the calculations to  $t = 25$ .

3. We say that  $x$  is stationary at the state  $(x,y)$  if, when  $x(t) = x$  and  $y(t) = y$ , then  $x(t + 1) = x(t)$ . Similarly, we define the states at which  $y$  is stationary.

Show on graph paper the set of states  $(x,y)$  at which  $x$  is stationary in the situations in Exercise 1. Show also, on the same sheet of graph paper, the states at which  $y$  is stationary. What is the intersection of these two sets of states?

4. In the situations in Exercise 1, what is the set of points  $(x,y)$  such that

$$x > 0, \quad y > 0,$$

and if  $x(t) = x$  and  $y(t) = y$ , then  $x(t+1) > x(t)$ ? These are the states at which  $x$  is increasing. What elementary geometric figure is formed by the points representing these states?

What elementary geometric figure is formed by the set of states  $(x,y)$  at which  $y$  is increasing?

5. Show on your graph paper the sets of points  $(x,y)$  at which  $x \geq 0$  and  $y \geq 0$ , which represent states at which

- (a)  $x$  and  $y$  are both increasing;
- (b)  $x$  is increasing and  $y$  is decreasing;
- (c)  $x$  is decreasing and  $y$  is increasing;
- (d)  $x$  and  $y$  are both decreasing;
- (e) the populations are at equilibrium.

6. Work Exercise 2 as far as  $t = 15$  using the values

$$a = 1, \quad b = .1, \quad c = .2,$$

$$A = .1, \quad B = .1, \quad C = .1.$$

Take  $h = 1$  and the initial state  $x = 2$  and  $y = 3$ . If you wish, you may think of  $x$  and  $y$  as measured in thousands. Notice that now the minnows are the main food supply for the pike, so that if there are not enough minnows, the pike die off.

7. Set up the general form of the equations describing the situation where two species, say pike and mackerel, prey on the minnows. Try at least one numerical experiment to see what happens if you assume different rates of excess births over deaths and of eating minnows for the two species.
8. Set up the general form of the equations describing the situation where the main food supply of the minnows consists of algae, and the minnows are the main food supply of the pike. Try at least one numerical experiment.

---

## 6. Summary and Some Extensions

In parts 2 and 3 we saw how the simple assumption of constant relative growth rate leads to the geometric progression as a mathematical description or model of growth for a single population. This model, when applied to human populations, is often referred to as the Malthusian model, after Thomas Malthus

see (6) . In Problem Set 4, Exercise 5 this model was expressed by the formula

$$x(t) = c^t x(0),$$

and we can see from the formula that when  $c > 1$ ,  $x(t)$  will be larger than any preassigned number if  $t$  is large enough. To avoid this "explosion" and make our model more realistic we can assume that the limits of the environment act to decrease the growth rate as the population size increases. A biologist might explain this by saying that as the population size increases, its ability to contaminate a closed environment also increases. If  $c$  represents this rate of contamination, we have

$$r = R - c x(t).$$

Experimentalists have found this model useful to describe the growth of fruit fly populations in a laboratory system (see Lotka (5), p. 69). As another example, the table below shows the population of the United States from 1790 to 1950 along with predicted values using the formula

$$x(t + h) = 1.31 + 1.26 x(t) - .00122 (x(t))^2,$$

where  $h = 10$ , expressed in years.

<u>Year</u>	<u>Population</u> (millions)	<u>Predicted</u>
1790	3.93	
1800	5.31	6.28
1810	7.24	7.98
1820	9.64	10.40
1830	12.87	13.38
1840	17.07	17.37
1850	23.19	22.51
1860	31.44	29.97
1870	38.56	39.85
1880	50.16	48.23
1890	62.95	61.64
1900	75.99	76.04
1910	91.97	90.32
1920	105.71	107.24
1930	122.78	121.29
1940	131.67	138.11
1950	150.69	146.59

What is predicted for 1960?

Finally, we considered two populations, one species preying on the other. This predator---prey relation required a pair of simultaneous equations to describe the changing population sizes. As mentioned in the Introduction, Volterra used a similar model to study the relationship between the numbers of sharks and soles in the Adriatic. A graph of these relations might look like Figure 1.

The equations for growth used above are called difference equations because they use the differences

$$\frac{x(t + h) - x(t)}{h}$$

In practice, the equations are often simpler to handle if we study the differences as  $h$  becomes very small. As  $h$  approaches zero the difference equation approaches what we call a differential equation. Differential equations are the ones used in the references; but you should be able to understand the examples given in these books with the ideas you have learned here. For further reading on difference equations, with other applications, see 3.

Still another way to extend what we have done here is to use a model which allows for the chance variation in the population size at any time. Such models work with the probability that the population will be of a certain size, rather than with the population size itself. Bartlett (1.) gives a complete account of these models.

Figure 1.

Movement along ABCDE represents increasing time.  $x$  = number of soles,  $y$  = number of sharks; numbers may represent thousands of animals. At B the sharks have just learned about the soles and begin to increase as their food supply increases. By the time D is reached, the sharks have eaten so much that they begin to die off from lack of food supply, allowing the soles to increase unmolested from A to B when the cycle begins all over again.

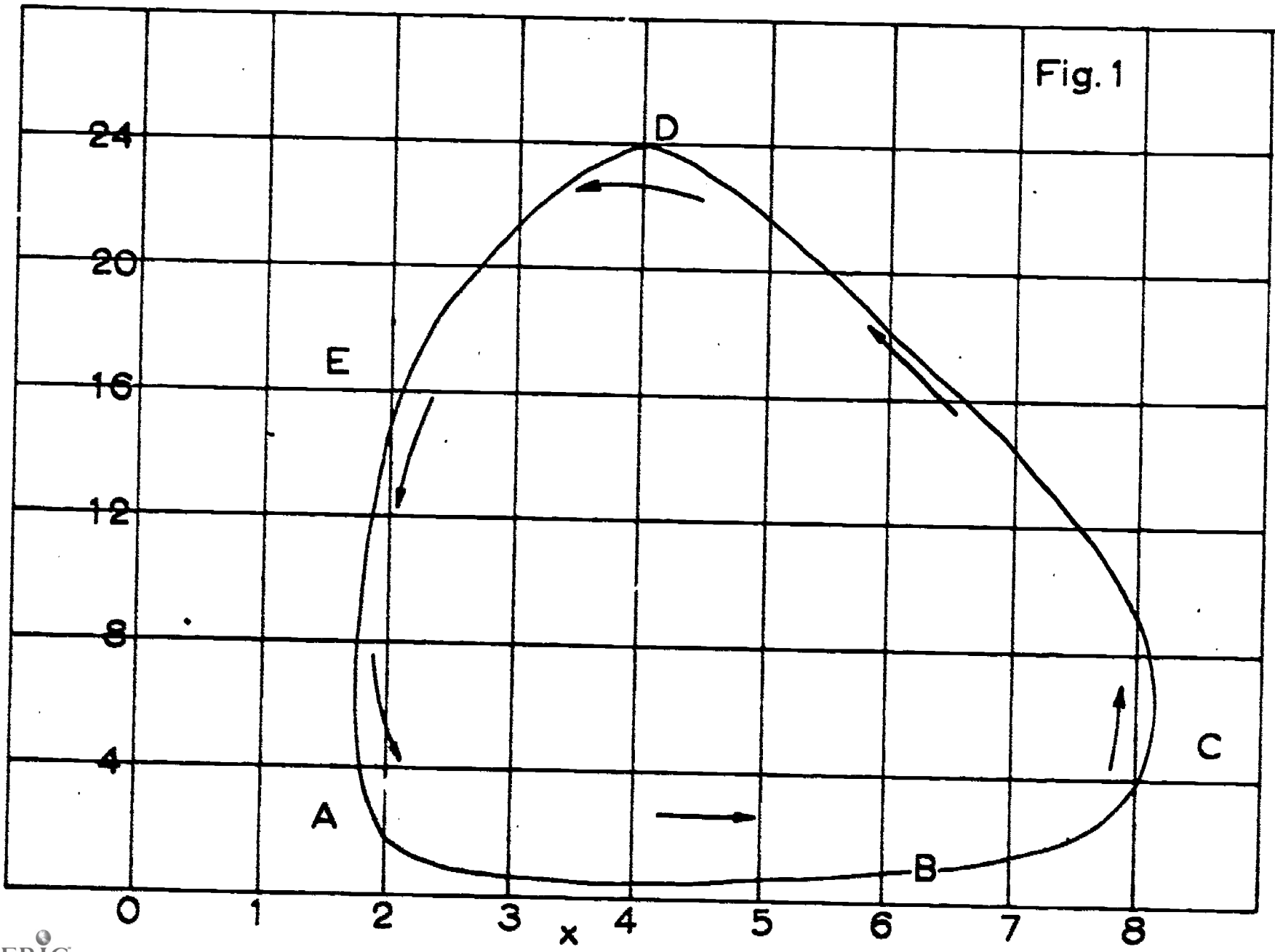
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Figure 1. is a rough graph of  $10x^{-4}e^x = 3.5e^{\frac{-y}{6}}$

Some points on the graph are:

x	y
1.8	6
2	1.8, 14.4
3	.9, 21
4	.7, 24
5	.8, 22
6	1.0, 18
7	1.6, 14.4
8	3.8, 9
8.2	6, 6

Fig. 1



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Answers

MATHEMATICAL THEORY OF THE STRUGGLE FOR LIFE

Problem Set 1

1.	t	x(t)	Change in Population	Relative Rate of Growth
	0	1,000,000		
	1	1,010,000	10,000	.01
	2	1,020,100	10,100	
	3	1,030,301	10,201	
	4	1,040,604	10,303	
	5	1,051,010	10,406	

$$2. \frac{x(1) - x(0)}{x(0)} = \frac{1,010,000 - 1,000,000}{1,000,000} = \frac{10,000}{1,000,000} = .01$$

$$\frac{x(2) - x(1)}{x(1)} = \frac{1,020,100 - 1,010,000}{1,010,000} = \frac{10,100}{1,010,000} = .01$$

$$\frac{x(t+1) - x(t)}{x(t)} = .01 \quad \text{correct to one significant digit.}$$

$$3. \frac{x(6) - x(5)}{x(5)} = .01$$

$$\frac{x(6) - 1,051,010}{1,051,010} = .01$$

$$x(6) = (.01)(1,051,010) + 1,051,010$$

$$x(6) = 1,061,520$$

$$4. x(7) = (.01)x(6) + x(6) = (1.01) x(6)$$

$$5. x(t) = \frac{x(t+1)}{r+1}$$



Problem Set 2

1.  $\frac{x(1) - x(0)}{x(0)} = .01$

$$x(1) - x(0) = (.01)x(0)$$

$$x(1) = (1.01)x(0)$$

In similar manner:

$$x(2) = (1.01)x(1)$$

$$x(3) = (1.01)x(2)$$

$$x(t+1) = (1.01)x(t)$$

2.  $x(2) = (1.01)x(1)$

$$x(2) = (1.01)(1.01)x(0)$$

$$x(2) = (1.01)^2 x(0)$$

3.  $x(3) = (1.01)(1.01)^2 x(0)$

$$x(3) = (1.01)^3 x(0)$$

$$x(4) = (1.01)^4 x(0)$$

$$x(5) = (1.01)^5 x(0)$$

4.  $x(t) = (1.01)^t x(0)$

5. (a)  $n$ th term =  $a r^{n-1}$

(b)  $(n+1)$ st term =  $a r^n$

(c)  $x(5)$  is the sixth term

(d)  $x(t)$  is the  $(t+1)$  term

Problem Set 3

$$\begin{aligned} 1. \quad x(1) &= r x(0) + x(0) \\ &= (r+1)x(0) \end{aligned}$$

$$\begin{aligned} x(2) &= r x(1) + x(1) \\ &= (r+1) x(1) \end{aligned}$$

$$\begin{aligned} x(t+1) &= r x(t) + x(t) \\ &= (r+1) x(t) \end{aligned}$$

$$2. \quad x(2) = (r+1) x(1) \quad \text{and} \quad x(1) = (r+1) x(0)$$

thus

$$\begin{aligned} x(2) &= (r+1)(r+1)x(0) \\ &= (r+1)^2 x(0) \end{aligned}$$

$$3. \quad x(3) = (1+r) x(2) \quad \text{and} \quad x(2) = (1+r)^2 x(0)$$

thus

$$x(3) = (1+r)^3 x(0)$$

$$4. \quad x(t) = (1+r)^t x(0)$$

$$5. \quad A = (1+r)^n P$$

6. Same pattern

Problem Set 4

1. (a)  $\frac{x(h) - x(0)}{h x(0)} = r$

$$x(h) = r h x(0) + x(0)$$

$$x(h) = (r h + 1)x(0)$$

(b)  $\frac{x(2h) - x(h)}{h x(h)} = r$

$$x(2h) = (r h + 1)x(h)$$

(c)  $\frac{x(3h) - x(2h)}{h x(2h)} = r$

$$x(3h) = (r h + 1)(x(2h))$$

(d)  $x(nh) = (r h + 1)x((n-1)h)$

(e)  $x((n+1)h) = (r h + 1)x(nh)$

2.  $x(h) = (rh+1)x(0)$

$$x(2h) = (rh+1)x(h)$$

$$x(3h) = (rh+1)x(2h)$$

$$x(nh) = (rh+1)x((n-1)h)$$

$$x((n+1)h) = (rh+1)x(nh)$$

3.  $x(h) = (rh+1)x(0)$

$$x(2h) = (rh+1)(rh+1)x(0)$$

$$x(2h) = (rh+1)^2 x(0)$$

$$x(3h) = (rh+1)(rh+1)^2 x(0)$$

$$= (rh+1)^3 x(0)$$

$$x(nh) = (rh+1)^n x(0)$$

$$4. x(nh) = (rh+1)^n x(0) \text{ and } t = nh$$

$$\therefore x(t) = (rh+1)^{\frac{t}{h}} x(0)$$

$$x(t) = c^t x(0)$$

$$5. c = (rh+1)^{\frac{1}{h}}$$

$$6. A(2t) = P\left(\frac{r}{2} + 1\right)^{2t} = c^t P, \text{ where } c = \left(\frac{1}{2}r+1\right)^2$$

$$A(4t) = P\left(\frac{r}{4} + 1\right)^{4t} = c^t P, \text{ where } c = \left(\frac{1}{4}r+1\right)^4$$

7.

r	h	c	r	h	c	r	h	c
1	1	2	.5	1	(1.5)	2	1	3
1	.5	(1.5) <sup>2</sup>	.5	.5	(1.25) <sup>2</sup>	2	.5	(2) <sup>2</sup>
1	.1	(1.1) <sup>10</sup>	.5	.1	(1.05) <sup>10</sup>	2	.1	(1.2) <sup>10</sup>
1	.01	(1.01) <sup>100</sup>	.5	.01	(1.005) <sup>100</sup>	2	.01	(1.02) <sup>100</sup>
1	.001	(1.001) <sup>1000</sup>	.5	.001	(1.0005) <sup>1000</sup>	2	.001	(1.002) <sup>1000</sup>

$$c = (rh+1)^{\frac{1}{h}}$$

$$8. c(r,h) = (rh+1)^{\frac{1}{h}}$$

$$c(1,.001) = (1.001)^{1000}$$

$$c(1,.001)^2 = (1.001)^{2000} \text{ and } c(2,.001) = (1.002)^{1000}$$

$$\therefore c(1,.001)^2 > c(2,.001)$$

$$c(.5,.001)^2 = (1.0005)^{2000} \text{ and } c(1,.001) = (1.001)^{1000}$$

$$c(.5,.001)^2 > c(1,.001)$$

Hint: Use binomial expansion for approximations.

9. (a) Prove If  $r > 0$  then  $(1+r)^2 > 1+2r$

Proof  $(1+r)^2 = 1+2r+r^2$

$$(1+r)^2 - (1+2r) = r^2$$

$$(1+r)^2 - (1+2r) > 0 \text{ since } r^2 > 0$$

$$\therefore (1+r)^2 > 1+2r \text{ Q.E.D. since } a > b \text{ iff } a - b > 0$$

(b) Prove If  $r > 0$  and  $(1+r)^n > 1+nr$ , then  $(1+r)^{n+1} > 1+(n+1)r$

Proof  $(1+r)^n > 1+nr \longrightarrow n > 0$

$$(1+r)^n(1+r) > (1+nr)(1+r)$$

$$(1+r)^{n+1} > 1+nr+r+nr^2$$

$$(1+r)^{n+1} > 1+(n+1)r+nr^2$$

$$(1+r)^{n+1} - [1+(n+1)r] > nr^2 > 0 \text{ since } n > 0, n \in \mathbb{I} \\ \text{and } r > 0$$

$$\therefore (1+r)^{n+1} > 1+(n+1)r \quad \text{Q.E.D.}$$

(c) Prove  $(1.000001)^{1,000,000,000} > 1.001$

$$\text{Let } n = 999,999,999 \text{ and } r = .000001$$

$$\text{then } (1+r)^{n+1} = (1.000001)^{1,000,000,000}$$

$$\text{thus } (1.000001)^{1,000,000,000} > 1+(999,999,999+1)(.000001)$$

$$(1.000001)^{1,000,000,000} > 1,001 > 1.001$$

$$\therefore (1.000001)^{1,000,000,000} > 1.001$$

(d)  $(n+1)(.000001) \geq 1,000,000$

$$\begin{cases} (n+1) \geq 1,000,000,000,000 \\ n \geq 1,000,000,000,001 \end{cases}$$

### Problem Set 5

1.  $\frac{x(t+h) - x(t)}{h} = R - c x(t)$

$$x(t+h) = (R h + 1) x(t) - h c (x(t))^2$$

2. If  $R = .01$ ,  $h = 1$ ,  $c = .000001$ ,  $x(0) = 1,000,000$

t	x(t)
0	1,000,000
1	10,000
2	10,000
3	10,000
4	10,000
5	10,000

3.

R	h	c	x(0)	x(1)	x(2)
.01	1	.000001	1,000,100	9,900	9,900
.01	1	.000001	900,000	100,000	90,000
.01	.5	.000001	1,000,100	500,000	400,000
.01	.01	.000001	1,000,100	1,000,000	1,000,000

Examples for Number 3.

$$R = .01, \quad h = 1, \quad c = .000001, \quad x(0) = 1,000,100$$

$$x(t+h) = (Rh+1)x(t) - hc(x(t))^2$$

$$x(1) = x(0+1) = ((.01)1 + 1)(1,000,100) - (1)(.000001)(1,000,100)^2$$

$$= 9,900.99$$

$$= \underline{9,900} \quad (2 \text{ significant figures})$$

$$x(2) = x(1+1) = ((.01)1 + 1)(9,900) - (1)(.000001)(9,900)^2$$

$$= \underline{9,900} \quad (2 \text{ significant figures})$$

$$R = .01, \quad h = .5, \quad c = .000001, \quad x(0) = 1,000,100$$

$$x(.5) = x(0 + .5) = ((.01)(.5) + 1)(1,000,100) - (.5)(.000001)(1,000,100)^2$$

$$= \underline{500,000} \quad (1 \text{ significant figure})$$

$$x(1) = x(.5+.5) = ((.01)(.5) + 1)(500,000) - (.5)(.000001)(500,000)^2$$

$$= 377,500$$

$$= \underline{400,000} \quad (1 \text{ significant figure})$$

4. The relative change of population,  $r = R - cx$ . Thus, if  $x = \frac{R}{c}$  then  $r = 0$ .

Problem Set 6

1. If  $x(t+h) = x(t)$  then

$$x(t) = (Rh + 1)x(t) - hc(x(t))^2$$

$$\therefore x(t) = 0 \text{ or } x(t) = \frac{R}{c}$$

The population at time  $t$  is zero or the relative change of population is zero.

2. Let  $E = \frac{R}{c}$ . If  $x(0) < E$  then

$$(a) \frac{x(h) - x(0)}{h x(0)} = R - c x(0) > R - c \left(\frac{R}{c}\right) = 0$$

$$x(h) > x(0)$$

(b)  $x(h)$  will remain greater than  $x(0)$

(c)  $x(t)$  approaches  $x(0)$

3. (a) If  $x(0) = \frac{1}{b}$  where  $b = hc$

$$\text{then } x(h) = \frac{Rh + 1}{hc} - \frac{hc}{(hc)^2}$$

$$= \frac{Rh}{hc} = \frac{R}{c}$$

(b) The relative rate of change is zero.

4. If  $\frac{1}{b} < x(0) < \frac{a}{b}$

$$y = ax - bx^2$$

$$y = -b \left( x^2 - \frac{a}{b}x + \frac{a^2}{4b^2} \right) + \frac{a^2}{4b} = -b \left( x - \frac{a}{2b} \right)^2 + \frac{a^2}{4b}$$

thus  $(a - 1) > x(h) > 0$

also  $(a - 1)(a - ab + b) > x(2h) > 0$

5. If  $x(0) > \frac{a}{b}$  then  $x(h) < 0$

6.  $z(t) = E - x(t)$  where  $E = \frac{R}{c}$

thus  $x(t) = E - z(t)$  so that

$$z(t+h) = E - x(t+h) = (1-Rh) z(t) + hc (z(t))^2$$

$$\underline{A = 1 - Rh} \quad \underline{B = hc}$$

7. Prove if  $|z(t)| < \frac{1-A}{B}$ , then  $|z(t+h)| < |z(t)|$

Proof

1) Assume the conclusion is false or  $|z(t)| < |z(t+h)|$

2)  $-|z(t+h)| < z(t) < |z(t+h)|$

3)  $z(t) < (1 - Rh) z(t) + hc (z(t))^2$  when  $z(t+h) \geq 0$

4)  $\frac{1 - (1-Rh)}{hc} < z(t)$  when  $z(t+h) \geq 0$

5)  $\frac{1 - A}{B} < z(t)$

6) But the hypothesis  $|z(t)| < \frac{1-A}{B} \iff -\frac{1-A}{B} < z(t) < \frac{1-A}{B}$

7) Thus, we have a contradiction so that  $|z(t+h)| \not> |z(t)|$

8)  $|z(t+h)| \neq |z(t)|$  since they could be equal only if  $hc = 0$  and  $Rh = 1$  which leads to  $c = 0$ . But  $c \neq 0$  since  $E = \frac{R}{c}$ .

9) Thus by the trichotomy property,  $|z(t+h)| < |z(t)|$ . Q.E.D.

### Problem Set 7

1.  $x(t+h) = x(t) (ah+1 - bh x(t) - ch y(t))$

$y(t+h) = y(t) (Ah+1 + Bh x(t) - Ch y(t))$



2. Example:

$$x(0+1) = x(1) = 16000 \left( (.05)(1) + 1 - (.000001)(16000) - (.00002)(2000) \right)$$

$$= 16000 (.994) = 15904 = 15,900 \text{ (to 3 significant figures)}$$

(NOTE: It is easier to multiply 16000 by .006 and subtract.)

$$y(0+1) = y(1) = 2000 \left( (.01) 1 + 1 + (.00001)(16000) - (.0001)(2000) \right)$$

$$= 1940. \text{ (to 3 significant figures).}$$

(Answers may vary somewhat depending upon the number of significant figures which are kept.)

t	x(t)	y(t)	t	x(t)	y(t)
0	16000	2000	13	15590	1685
1	15900	1940	14	15600	1680
2	15800	1890	15	15610	1677
3	15700	1850	16	15625	1675
4	15650	1820	17	15640	1673
5	15620	1790	18	15655	1671
6	15600	1765	19	15670	1670
7	15580	1745	20	15685	1669
8	15570	1730	21	15700	1669
9	15570	1720	22	15715	1669
10	15570	1710	23	15730	1670
11	15570	1700	24	15745	1670
12	15580	1692	25	15760	1671

3.  $x(t) = x(t+1)$  when  $x = 0$  or  $x = \frac{a-cy}{b}$

$y(t) = y(t+1)$  when  $y = 0$  or  $y = \frac{A+Bx}{C}$

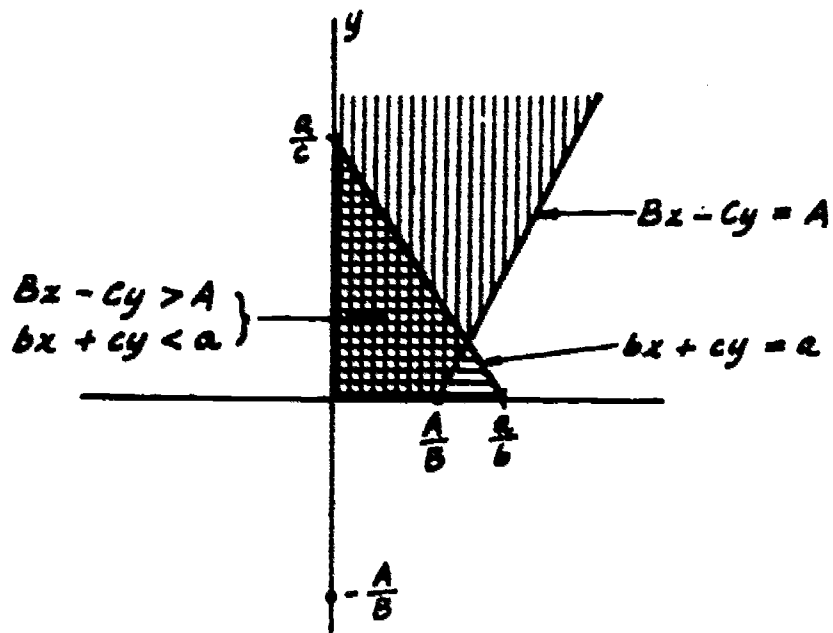
Intersection of the two sets is  $y = \frac{Ab+Ba}{Cb+Bc}$

$x = \frac{Ca-Ac}{Cb+Bc}$

4. (a)  $b x + c y < a$

(b)  $B x - C y > A$

5.



The remaining parts of 5 follow from the above figure.

6.

t	x(t)	y(t)	t	x(t)	y(t)
0	2	3	8	2.58	3.86
1	2.4	3	9	2.50	3.75
2	2.78	3.12	10	2.50	3.66
3	3.06	3.34	11	2.52	3.60
4	3.14	3.57	12	2.59	3.57
5	3.05	3.78	13	2.65	3.58
6	2.97	3.89	14	2.70	3.61
7	2.75	3.93	15	2.72	3.64

7. If  $x(t)$  represents the population of the minnows at time  $t$   
 $y(t)$  represents the population of the pike at time  $t$   
 $z(t)$  represents the population of the mackerel at time  $t$   
then

$$x(t+h) = x(t) (a h + 1 - c y(t) - d z(t) - b x(t))$$

where  $r_x = a - bx - cy - dz$  and  $a, b, c, d$  are positive constants.

Also

$$r_y = A + Bx(t) - Cy(t) - Dz(t) = \frac{y(t+h) - y(t)}{h y(t)}$$

also

$$r_z = \alpha + \beta x(t) - \gamma y(t) - \delta z(t) = \frac{z(t+h) - z(t)}{h z(t)}$$

8.  $x$  = population of algae at time  $t$   
 $y$  = population of minnows at time  $t$   
 $z$  = population of pike at time  $t$

$$r_x = a - bx - cy + dz$$

$$r_y = A - By + cx - Dz$$

$$r_z = \alpha - \beta z + \gamma y$$

Thus for example

$$a - bx(t) - cy(t) + dz(t) = \frac{x(t+h) - x(t)}{hx(t)}$$