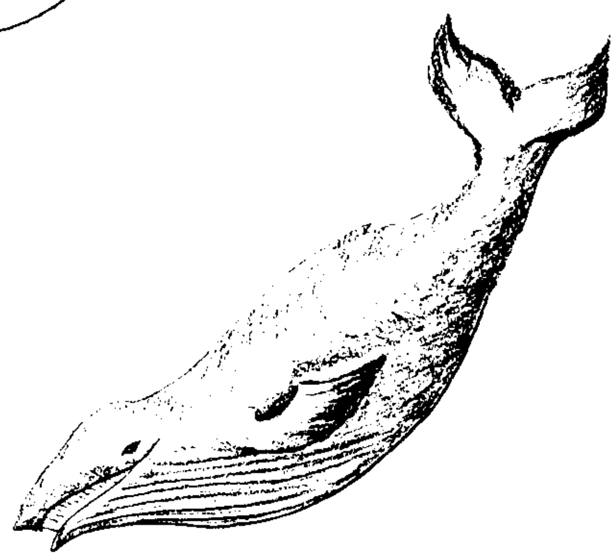
UMAP

UNIT 610

MODULES AND MONOGRAPHS IN UNDERGRADUATE MATHEMATICS AND ITS APPLICATIONS PROJECT

WHALES AND KRILL: A MATHEMATICAL MODEL

by Raymond N. Greenwell



APPLICATIONS OF DIFFERENTIAL EQUATIONS TO ECOLOGY

Intermodular Description Sheet: UMAP Unit 610

Title: WHALES AND KRILL: A MATHEMATICAL MODEL

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Mathematics Field: Differential equations, mathematical modeling

Application Field: Ecology

Abstract: A predator-prey system involving whales and krill is modeled by a system of differential equations. Although the equations are not solvable, information is extracted using dimensional analysis and the study of equilibrium points. The concept of maximum sustainable yield is introduced and used to draw conclusions about fishing strategies. Students learn to construct a differential equation model, remove dimensions from a set of equations, find equilibrium points of a system of differential equations and learn their significance, learn about maximum sustainable yield and use it to draw conclusions about fishing strategies, and practice manipulative skills in algebra and calculus.

Prerequisites:

1. Ability to differentiate algebraic expressions.
2. Knowledge of integration techniques.
3. Knowledge of maxima-minima techniques of calculus.
4. Familiarity with the concept of units or dimensions.

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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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1. INTRODUCTION

Ever since Thomas Malthus proposed in 1798 that the world population increases exponentially, mathematical models have been used to study the growth and decay of populations. One model, developed by Robert M. May, John R. Beddington, Colin W. Clark, Sidney J. Holt and Richard M. Laws, (see the reference section), involves the relationship of baleen whales with their food, the Antarctic krill.

Baleen whales are generally the largest of the whales. They include the blue whale which, at a length of up to 30 meters, can truly be called the king of the whales (not to be confused with the Prince of Wales). They are toothless, equipped instead with horny plates known as baleen (from a Greek word for mustache), which hang from the roof of their mouth. The baleen act as a sieve to strain food out of the water. A favorite food of baleen whales is the Antarctic krill, a shrimplike creature about two inches long. From January to April, the density of krill in the Antarctic Ocean can be as high as 20 kilograms of krill per cubic meter of ocean. Any whale unwilling to search after such an abundant source of food must certainly be labeled a ne'er-do-whale.

The number of baleen whales has been drastically reduced by excessive hunting. As a result, there is a surplus of krill, and people have begun harvesting the krill, a rich source of vitamin A, as an alternative food source. The krill are also consumed by many other ocean creatures, however, and the effect on these creatures, as well as on the already depleted baleen whales, is a cause for concern (this could be referred to as a problem of over-krill). One way to predict the effect of various fishing strategies is to study a mathematical model of the situation. In this module we will look at the model studied by May et al. and rederive some of their results.

2. THE MODEL

Let N_1 be the population of the krill, which represents the prey in this predator-prey model, and let N_2 be the population of the whales (the predators). We will first write a differential equation describing the growth and decay of the krill, and then we will write a similar equation for the whales.

The simplest form of population growth is based on the assumption that a population grows at a rate proportional to its own size; that is, twice as large a population will produce twice as many babies. Mathematically,

$$\frac{dN_1}{dt} = r_1 N_1, \tag{1}$$

where r_1, the positive constant of proportionality, represents the rate of growth.

Exercise 1. Show that Equation (1) implies exponential growth of the krill.

Equation (1) is unrealistic because krill cannot grow without bound. Beyond a certain population size, known as the carrying capacity of the environment, the krill will have insufficient plankton to eat. If we denote the carrying capacity by K, then Equation (1) can be modified as

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K}\right). \tag{2}$$

This equation is known as the logistic equation.

Exercises

2. Show that

   a) if N_1 is small, Equation (2) is essentially the same as Equation (1);
   b) as N_1 grows closer to K, the growth rate dN_1/dt declines;
   c) if N_1 is greater than K, the population decreases. What happens if N_1 is equal to K?

3. Solve Equation (2) for N_1 as a function of t.

Equation (2) would be a fairly realistic model were it not for the whales eating the krill. The hungry whales will decrease growth at a rate proportional to their number: twice as many whales will eat twice as many krill. Furthermore, this decrease should be proportional to the number of krill: doubling the amount of krill doubles the chance that the whales will find the krill and eat them. (Although this last statement is probably not true for extremely large krill populations, the model we have described is fairly realistic without becoming so complex as to be impossible to study.) Our equation is now

(3) $$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K}\right) - CN_1 N_2 ,$$

where C is a positive constant representing the rate at which the whales consume the krill (i.e., each whale consumes CN_1 krill per unit time).

We now turn to the whales. Their growth rate can also be described by a logistic equation, but the carrying capacity of the whales is limited by how much food they have to eat, which is proportional to the krill population. Thus, in place of a constant K, we will have the expression αN_1, where α is a positive constant expressing how many whales can be sustained on a population of one krill. (Answer: not very many, so α is very small.) The equation for the whales is thus

(4) $$\frac{dN_2}{dt} = r_2 N_2 \left(1 - N_2/(\alpha N_1)\right) .$$

It would be nice at this point if we could solve Equations (3) and (4). But unlike Equations (1) and (2), these equations cannot be solved analytically. We can, however, give some qualitative results, even if the exact answers cannot be found.

3. THE FISHERMAN COMETH

Since one of the main purposes of this model is to examine the effects of various fishing strategies, we should introduce terms into our equations describing the effects of fishing. Let us denote the fishing effort for krill and whale by F_1 and F_2, respectively. We will scale the fishing effort to make $F_1 = 1$ and $F_2 = 1$ correspond to an effort which yields at a rate proportional to the natural growth rate. The krill yield can then be expressed as $Y_1 = r_1 F_1 N_1$ (note that $F_1 = 1$ implies $Y_1 = r_1 N_1$, which is the natural growth rate according to Equation (1)), and the whale yield is similarly expressed as $Y_2 = r_2 F_2 N_2$. Equations (3) and (4) become

(5) $$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K}\right) - CN_1 N_2 - r_1 F_1 N_1 ,$$

(6) $$\frac{dN_2}{dt} = r_2 N_2 \left(1 - N_2/(\alpha N_1)\right) - r_2 F_2 N_2 .$$

4. REMOVING THE DIMENSIONS

The model as designed would give different numerical answers for different units of measurements. Since we do not know the exact numbers anyway, it is simpler to represent the krill and whale populations in dimensionless form as

$$(7)\qquad X_1 = N_1/K$$
$$X_2 = N_2/(\alpha K).$$

Recall that K is the carrying capacity of the krill, so that $X_1 = 1$ (not 1 kilogram, not 1 ton, just 1) corresponds to a krill population equal to the maximum that the environment can sustain. Notice also that since both N_1 and K have dimensions [krill], X_1 has dimensions [krill]/[krill] = 1; that is, X_1 is dimensionless. The quantity N_2 has dimensions [whales] and α has dimensions [whales/krill] (this follows from the original definition of α), so X_2 has dimensions [whales]/([whales/krill] × [krill]) = [1], so X_2 is also dimensionless.

Exercises

4. Substitute (7) into Equations (5) and (6) and show

$$(8)\qquad \frac{dX_1}{dt} = r_1X_1(1 - F_1 - X_1 - \nu X_2)$$

$$(9)\qquad \frac{dX_2}{dt} = r_2X_2(1 - F_2 - X_2/X_1)$$

where ν is the dimensionless parameter

$$(10)\qquad \nu = C\alpha K/r_1.$$

5. Show that ν is dimensionless. Do this by calculating the dimensions of C, α, K, and r_1 (e.g., C must have units [1/(whales × time)] for Equation (3) to be correct), and then show that all the dimensions in Equation (10) cancel out.

We have now reduced the number of relevant parameters to three: r_1, r_2, and ν. This means that C, α, and K are not individually relevant. According to Equation (10), only their product is important.

Exercises

6. Notice from Equation (10) that if C is doubled and α halved, ν stays the same, so the model does not change. Explain what this means biologically.

7. Repeat Exercise 6, except this time consider doubling C and halving K.

8. Repeat Exercise 6, except this time double α and halve K.

5. LOOKING FOR EQUILIBRIUM POINTS

Since we cannot solve Equations (8) and (9), we will try to derive qualitative information. In particular, we will look for equilibrium points, which are values of X_1 and X_2 such that $dX_1/dt = 0$ and $dX_2/dt = 0$. In other words, if X_1 and X_2 are at an equilibrium point, they will stay there forever, since their derivatives are 0. We can easily find one equilibrium point from (8) and (9): let $X_1 = X_2 = 0$. Indeed, if there are no whales and no krill, the situation will stay that way forever. This accurately models life on the moon, but is not of great interest to us (or to the whales and krill!).

Exercise

9. Show from Equations (8) and (9) that if $X_1 > 0$ and $X_2 > 0$, and F_1 and F_2 are both less than 1, there is a unique equilibrium point:

$$X_1^* = \frac{1 - F_1}{1 + \nu(1 - F_2)} \tag{11}$$

$$X_2^* = \frac{(1 - F_1)(1 - F_2)}{1 + \nu(1 - F_2)}. \tag{12}$$

Another topic of interest is stability. Suppose X_1 and X_2 are close to the values given by Equations (11) and (12), but not exactly equal to them. Will the solution tend to move closer to the equilibrium point or farther away? The answer is that it would move closer, which implies that the equilibrium point is stable. (To see how this is proven, see, for example, Boyce, Wm. E. and DiPrima, Richard C., Elementary Differential Equations, John Wiley & Sons, 1977, Chapter 8.) If this were not so, the equilibrium point would never be observed, since it is highly unlikely that X_1 and X_2 would ever take on exactly the values given by (11) and (12).

6. THE EFFECT OF FISHING

In deriving Equations (11) and (12), we assumed that F_1 and F_2 are less than 1, meaning that the fish are being caught at a rate smaller than their natural replacement rate. If this were not the case, we would derive different equations.

Exercises

10. Use Equations (8) and (9) to determine what would happen if $F_1 < 1$ and $F_2 > 1$.

11. What would happen if $F_1 > 1$ and $F_2 > 1$?

12. Recall that the krill and whale yield were $Y_1 = r_1F_1N_1$ and $Y_2 = r_2F_2N_2$. Show from Equations (11) and (12) that the equilibrium krill and whale yield are

$$Y_1^* = \frac{(r_1K)\, F_1\, (1 - F_1)}{1 + \nu\,(1 - F_2)} \tag{13}$$

$$Y_2^* = \frac{\alpha r_2 K(1 - F_1)\, F_2\, (1 - F_2)}{1 + \nu\,(1 - F_2)}. \tag{14}$$

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7. MAXIMUM SUSTAINABLE YIELD

The concept of maximum sustainable yield is very important in ecosystem modeling. The maximum sustainable yield is the greatest harvest possible which can be continued indefinitely. In other words, if one tried to capture more of a species than the maximum sustainable yield, the population of the species would decrease, and either the harvest would have to decrease or the species would become extinct.

Equations (13) and (14) give sustainable yields, since they correspond to the equilibrium populations of the krill and the whales. It is of no value to maximize each one separately, since the two are interrelated, and making one larger may make the other smaller. In fact, we can see from Equation (13) that Y_1^* is maximized by making F_2 as large as possible, that is, by letting $F_2 = 1$. But then Equation (14) tells us that $Y_2^* = 0$. In other words, to maximize the krill yield, we would harvest the whales to extinction, since then there would be no whales to compete with us for the krill.

<u>Exercises</u>

13. Show that for fixed F_2, the krill yield is maximized by letting $F_1 = 0.5$.

14. Show that for fixed F_1, the whale yield is maximized by letting

(15) $$F_2 = \frac{(1 + \nu) - \sqrt{1 + \nu}}{\nu} \text{ when } \nu \neq 0.$$

Our answer to Exercise 13 can be used to shed some light on the meaning of ν. First of all, let us ignore the effect of the whale on the krill by letting $\nu = 0$ (notice from Equation (8) that if $\nu = 0$, the equation for X_1 does not involve X_2). Now we use the value $F_1 = 0.5$, which was found in Exercise 13 to give the maximum sustainable yield of krill, and then Equation (11) tells us that $X_1^* = 0.5$. Next, let us ignore the effect of fishing by letting $F_1 = F_2 = 0$; Equation (11) then gives

(16) $$X_1^* = \frac{1}{1 + \nu}.$$

We again get the value $X_1^* = 0.5$ if $\nu = 1$. This gives the following interpretation of ν: if $\nu = 1$, the whales are consuming the krill at the point of maximum sustainable yield. It is not currently known whether ν is less than, equal to, or greater than 1.

<u>Exercise 15</u>. Evaluate F_2 from Equation (15) for $\nu = 0.001$, 1, and 5.

You will notice in Exercise 15 that as ν increases, so does F_2. This means that as the rate at which the whales consume the krill increases, the whales should be sought with greater effort to achieve the maximum sustainable yield. That makes sense, since the whales would have a greater tendency to use up their supply of krill and starve themselves if their population were not held in check by fishing.

8. TOTAL VALUE

The best fishing policy would be to maximize total yield, which can be expressed as

(17) $$Y = Y_1^* + \gamma Y_2^*$$

where γ is a constant representing the relative value of the whales and the krill. Large values of γ cause a small increase in the whale yield, Y_2^*, to result in a large increase in the total yield, Y. This indicates that it is the whales that are valuable, rather than the krill. Similarly, small values of γ indicate that it is the krill that are more valuable.

Exercise

16. Show that Y can be written as

(18) $$Y = \frac{Kr_1(1 - F_1)(F_1 + \beta F_2(1 - F_2))}{1 + \nu(1 - F_2)},$$

where $\beta = \gamma\alpha(r_2/r_1)$.

You may wish to try maximizing the total yield, as given by Equation (18), by finding the optimum value of F_1 for a fixed F_2, substituting the result into Equation (18), and then solving for the optimum value of F_2. (If you are familiar with multivariable calculus, you can get the same result by setting the partial derivatives of Y equal to 0.) Unfortunately the algebra is cumbersome and the result not particularly enlightening. Instead, let us notice that if β is very large, Equation (18) becomes

(19) $$Y \approx \frac{Kr_1(1 - F_1)\beta F_2(1 - F_2)}{1 + \nu(1 - F_2)}.$$

We have ignored the F_1 term which is small compared to $\beta F_2(1 - F_2)$. If β is very small, Equation (18) becomes

(20) $$Y \approx \frac{Kr_1(1 - F_1)F_1}{1 + \nu(1 - F_2)}.$$

The value of F_1 that maximizes the right side of (19) is $F_1 = 0$, since F_1 appears only in the factor $(1 - F_1)$. The right side of (20) is maximized by making F_2 as large as possible. In other words, if β is large, it is best not to fish krill at all and leave them for the valuable whales to eat. But if β is small, we may as well harvest the whales to extinction so they will not compete with us for the valuable krill. It is only for intermediate values of β that the optimum fishing strategy involves both species.

9. CONCLUSIONS

To establish specific numerical solutions for F_1 and F_2, it would be necessary to measure ν and β. This may be extremely difficult, if not impossible, to accomplish. To calculate ν, for example, we would need to know r_1, the natural growth rate of the krill, and K, the saturation population of the krill. These might be determined through extensive measurements of the krill population in the absence of whales. The other components of ν, namely C and α, are even more difficult to measure, since they involve the interaction of the two species, as given by the analytically unsolvable Equations (5) and (6). Measuring β has an additional problem: our estimates of γ may be heavily value-laden. How can we measure the worth of an animal that is in danger of total extinction? Our answer depends upon how much we care about preserving the biological heritage of this planet.

Despite these difficulties, we do have qualitative results, such as our conclusion from the last section that, for many values of the relative worth of the whales and krill, the optimum strategy involves only one of the species. Furthermore, we have a quantitative framework in which to further our research.

10. REFERENCES

There is a great deal of literature on mathematical models of predator-prey systems. Many references can be found in the article by Robert M. May, John R. Beddington, Colin W. Clark, Sidney J. Holt, and Richard M. Laws, "Management of Multispecies Fisheries," Science, Vol. 205, 1979, pp. 267-277. The interested reader may want to start with the following books:

Gause, G.F., The Struggle for Existence, Dover, 1971 (originally published by Williams and Wilkins in 1934). Chapter III of this classic, entitled "The struggle for existence from the point of view of the mathematician," is closely related to the material in this module.

Gold, Harvey J., Mathematical Modeling of Biological Systems--an Introductory Guidebook, Wiley-Interscience, 1977. In addition to Section 7.5 on predator-prey systems, this book is full of principles for constructing and analyzing biological models in general.

Levin, S., ed., Lecture Notes in Biomathematics, Springer Verlag. Out of this series of thirteen volumes of articles, Volume 2 (Mathematical Problems in Biology, edited by Pauline van den Driessche, 1974) and Volume 13 (Mathematical Models of Biological Discovery, edited by D.L. Solomon and C. Walter, 1977) have the most to offer to the student of mathematical ecology.

Lotka, Alfred, Elements of Mathematical Biology, Dover, 1956 (originally published as Elements of Physical Biology, Williams and Wilkins, 1924). A bibliography on predator-prey systems would not be complete without this seminal work, whose author is commemorated by the famous Lotka-Volterra equations.

Pielou, E.C., An Introduction to Mathematical Ecology, Wiley-Interscience, 1969. Especially see Chapters 5 and 6 on two species interactions.

Smith, J. Maynard, Mathematical Ideas in Biology, Cambridge University, 1971, and Models in Ecology, Cambridge University, 1974. Both books, though small, have a great deal on population models.

Lectures on Mathematics in the Life Sciences, American Mathematical Society, Vol. 1: Some Mathematical Problems in Biology (1968) and Vol. 2: Some Mathematical Questions in Biology (1970). See especially the article by Leigh in Volume 1 and the article by MacArthur in Volume 2.

11. ACKNOWLEDGEMENTS

I would like to thank Robert M. May, John R. Beddington, Colin W. Clark, Sidney J. Holt and Richard M. Laws, who did the research paper upon which this module is based. I would also like to thank Philip Tuchinsky for his help in getting me started, and to my wife Karla for her editorial assistance and her whale drawing.

12. ANSWERS TO EXERCISES

1. $\frac{dN_1}{dt} = r_1 N_1$.

Separating variable yields

$$\int \frac{dN_1}{N_1} = \int r_1 dt \rightarrow \ln|N_1| = r_1 t + C$$

$$N_1 = \pm e^{r_1 t + C} = \pm e^C e^{r_1 t} = ke^{r_1 t}$$

where k could be either e^C or $-e^C$. Since N_1 represents a population, k must be positive.

2. a) $\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K}\right)$.

If N_1 is small, $1 - N_1/K \approx 1$, so

$$\frac{dN_1}{dt} = r_1 N_1,$$

which is the equation of exponential growth.

b) As N_1 approaches K, the expression $1 - N_1/K$ approaches 0, so the growth rate, dN_1/dt, also approaches 0.

c) If N_1 is greater than K, the expression $1 - N_1/K$ is negative, so the growth rate, dN_1/dt, is negative.
If $N_1 = K$, then $dN_1/dt = 0$, so the population remains constant.

3. Separating variables, we find that

$$\int \frac{dN_1}{N_1 \left(1 - \frac{N_1}{K}\right)} = \int r_1 dt$$

$$\int \frac{KdN_1}{N_1(K - N_1)} = r_1 t + C.$$

Using partial fractions on the left gives

$$\int \left(\frac{A}{N_1} + \frac{B}{K - N_1}\right) dN_1$$

where

$$A = \frac{K}{K - N_1}\Bigg|_{N_1=0} = 1 \text{ and } B = \frac{K}{N_1}\Bigg|_{N_1=K} = 1.$$

Thus,

$$\ln|N_1| - \ln|K - N_1| = \ln\left|\frac{N_1}{K - N_1}\right| = r_1t + C$$

$$\left|\frac{N_1}{K - N_1}\right| = e^{r_1t+c} = e^c e^{r_1t}$$

$$\frac{N_1}{K - N_1} = Ae^{r_1t},$$

where $A = \pm e^c$ is negative if $N_1 > K$ and positive if $N_1 < K$. Accordingly,

$$N_1 = KAE^{r_1t} - N_1Ae^{r_1t}$$

$$N_1 + N_1Ae^{r_1t} = KAe^{r_1t}$$

$$N_1 = \frac{KAe^{r_1t}}{1 + Ae^{r_1t}} - \frac{1/Ae^{r_1t}}{1/Ae^{r_1t}}$$

$$= \frac{K}{1 + Be^{-r_1t}},$$

where $B = 1/A$.

4. $N_1 = KX_1$, $N_2 = \alpha KX_2$

$$\frac{dN_1}{dt} = K\frac{dX_1}{dt} = r_1KX_1\ (1 - X_1) - CKX_1\alpha KX_2 - r_1F_1KX_1.$$

Upon dividing by K we find that

$$\frac{dX_1}{dt} = r_1X_1\ (1 - X_1 - \frac{C\alpha K}{r_1}X_2 - F_1).$$

Setting $C\alpha K/r_1 = \nu$ yields Equation (8). To derive Equation (9), observe that

$$\frac{dN_2}{dt} = \alpha K\frac{dX_2}{dt} = r_2\alpha KX_2\ (1 - \alpha KX_2/(\alpha KX_1)) - r_2F_2\alpha KX_2.$$

Dividing by αK yields

$$\frac{dX_2}{dt} = r_2X_2(1 - X_2/X_1 - F_2).$$

5. According to Equation (3), r_1 must have units [1/time] and K must have units [krill]. According to Equation (4), α must have units [whales/krill]. Thus, ν has dimensions

$$\frac{[1/(\text{whales} \times \text{time})] \times [\text{whales/krill}][\text{krill}]}{[1/\text{time}]} = [1].$$

6. If the rate that the whales eat the krill is doubled but the number of whales is halved, there would be no overall change in the situation. The number of whales could be halved if their carrying capacity (αN_1) was cut in half.

7. If the whales eat the krill at double their original rate, but there are only half as many krill to eat, the situation would remain the same.

8. If the carrying capacity of the whales doubled, the situation would remain the same if the number of krill also doubled. This would be accomplished if the carrying capacity of the krill is doubled.

9. Since $X_1 \neq 0$ and $X_2 \neq 0$, Equations (8) and (9) imply

$$1 - F_1 - X_1 - \nu X_2 = 0,$$

$$1 - F_2 - X_2/X_1 = 0.$$

Solving the second equation for X_2 yields

$$(1 - F_2)X_1 = X_2.$$

Substituting into the first equation yields

$$(1 - F_1) - X_1 - \nu(1 - F_2)X_1 = 0$$

$$1 - F_1 = X_1(1 + \nu(1 - F_2))$$

$$X_1 = \frac{1 - F_1}{1 + \nu(1 - F_2)}$$

and

$$X_2 = (1 - F_2)X_1 = \frac{(1 - F_1)(1 - F_2)}{1 + \nu(1 - F_2)}.$$

10. If $F_1 < 1$ and $F_2 > 1$, then

$$\frac{dX_2}{dt} = r_2X_2\ (1 - F_2 - X_2/X_1) < -r_2(X_2)^2/X_1,$$

so the whale population would decrease. Then dX_1/dt would increase, since νX_2 would become smaller, so the krill population would either increase more quickly or decrease more slowly, depending on the value of F_1.

11. If we also have $F_1 > 1$, then

$$\frac{dX_1}{dt} = r_1X_1\ (1 - F_1 - X_1 - \nu X_2) < - r_1X_1\ (X_1 + \nu X_2),$$

so the krill population will also decrease.

12. $Y_1* = r_1F_1N_1*$

$$= r_1F_1KX_1*$$

$$= \frac{r_1F_1K\ (1 - F_1)}{1 + \nu(1 - F_2)}.$$

$Y_2* = r_2F_2N_2*$

$$= r_2F_2\alpha KX_2*$$

$$= \frac{r_2F_2\alpha K\ (1 - F_1)(1 - F_2)}{1 + \nu(1 - F_2)}.$$

13. From (13),

$$\frac{dY_1*}{dF_1} = \left[\frac{r_1K}{1 + \nu(1 - F_2)}\right]\left[1 - 2F_1\right] = 0,$$

which implies that $F_1 = 0.5$.

14. $$\frac{dY_2*}{dF_2} = \frac{[\alpha r_2K(1 - F_1)]\ [(1 + \nu(1 - F_2))(1 - 2F_2) - (F_2-(F_2)^2)(-\nu)]}{[1 + \nu(1 - F_2)]^2} = 0$$

$$1 - 2F_2 + \nu(1 - 3F_2 + 2(F_2)^2) + \nu F_2 - \nu(F_2)^2 = 0$$

$$(1 + \nu) + F_2(-2 -2\nu) + \nu(F_2)^2 = 0.$$

Therefore,

$$F_2 = \frac{2 + 2\nu \pm \sqrt{(-2 - 2\nu)^2 - 4(1 + \nu)\nu}}{2\nu}$$

$$= \frac{2(1 + \nu) \pm 2\sqrt{1 + 2\nu + \nu^2 - \nu - \nu^2}}{2\nu}$$

$$= \frac{1 + \nu \pm \sqrt{1 + \nu}}{\nu}.$$

To decide whether the $\pm$ is plus or minus, notice that the last equation can be written

$$F_2 = 1 \pm \frac{1}{\nu} + \frac{\sqrt{1+\nu}}{\nu}.$$

Since F_2 must be no larger than 1, and since ν must be positive, the sign must be negative.

15. If $\nu = 0.001$, then

$$F_2 = \frac{1.001 - \sqrt{1.001}}{.001}$$

$$= 0.5001.$$

You should notice in the second line of the answer to Exercise 14 that if $\nu = 0$, then $F_2 = 0.5$.

If $\nu = 1$, then $F_2 = \frac{2 - \sqrt{2}}{1} = 0.586$.

If $\nu = 5$, then $F_2 = \frac{6 - \sqrt{6}}{5} = 0.710$.

16. $Y = Y_1^* + \gamma Y_2^*$

$$= \frac{(r_1K)\, F_1\, (1 - F_1)}{1 + \nu(1 - F_2)} + \frac{\gamma\alpha r_2 K\, (1 - F_1)\, F_2\, (1 - F_2)}{1 + \nu(1 - F_2)}$$

$$= \frac{Kr_1(1 - F_1)(F_1 + \gamma\alpha r_2 F_2\, (1 - F_2)/r_1)}{1 + \nu(1 - F_2)}$$

$$= \frac{Kr_1(1 - F_1)(F_1 + \beta F_2\, (1 - F_2))}{1 + \nu\, (1 - F_2)},$$

where $\beta = \gamma\alpha(r_2/r_1)$.