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Qualitative Analysis of a Resource Management Model and Its Application to the Past and Future of Endangered Whale Populations

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Abstract: Observed whale dynamics show drastic historical population declines, some of which have not been reversed in spite of restrictions on harvesting. This phenomenon is not explained by traditional predator prey models, but we can do better by using models that incorporate more sophisticated assumptions about consumer-resource interaction. To that end, we derive the Holling type 3 consumption rate model and use it in a one-variable differential equation obtained by treating the predator population in a predator-prey model as a parameter rather than a dynamic variable. The resulting model produces dynamics in which low and high consumption levels lead to single high- and low-level stable resource equilibria, respectively, while intermediate consumption levels result in both high and low stable equilibria. The phase-line analysis is made more transparent by applying a particular structure to the function that gives the derivative in terms of the state. By positing a consumption level that starts low, gradually increases through technological change and human population growth, and decreases as a result of public policy, we are able to tell a story that explains the unexpectedly rapid decline of some resources, such as whales, followed by limited recovery in response to conservation. The analysis also offers guidelines for how to establish sustainable harvesting for restored populations. We include a bifurcation analysis and suggestions for how to teach the material with three different levels of focus on the modeling aspect of the study.

1 Introduction

Case studies play an important role in student learning by embedding the mathematics into non-mathematical contexts. The more interesting the context is to students, the more engaged they will be in the case study. The example presented here grew out of my interest in constructing a case study for a first-order differential equation that would use phase-line analysis to obtain qualitative behavior for a model that many students would find interesting. phase-line analysis is (or at least can be) presented early in a differential equations course, which allows the instructor to assign the case study before students reach the point of being overwhelmed by a full schedule. A secondary point of the case study is that it shows the relatively limited value of analytical solution methods for anything more complicated than the linear equations of radioactive decay and mechanical vibration. While an implicit solution formula can be found for any autonomous first-order equation, such a formula is not as useful as phase-line analysis for obtaining qualitative results nor as easy to use for solution graphs as numerical methods.

The key insight that led to the case study presented here is that any predator-prey model can be recast as a resource management model by assuming the 'predator' density is a control parameter rather than a dependent variable, as is the case where the number of harvesters in a system is controlled by policy rather than by population dynamics. It was only after doing the analysis that I saw that the results could be incorporated into a narrative setting involving the history of whale populations. There is insufficient data to determine accurate parameter values; instead, the goal of the investigation is to formulate a theory that can potentially explain the qualitative features of the observed population history.

Just what these qualitative features are is not completely clear. Several dates stand out as important in the history of whale populations [9]. Commercial whaling hit a peak in the early 1900s roughly between 1904 and 1916 and subsequently declined because of diminished stocks. The first attempt to regulate whaling was the International Agreement for the Regulation of Whaling of 1937. This agreement made very little impact, but was followed by a set of international regulations approved by the newly formed International Whaling Commission in 1946. In spite of the new regulations, whale populations continued to decline, leading to a public "Save the Whales" campaign instituted by the World Wildlife Fund in 1961. This exerted public pressure on countries to limit whaling, but the effect was still not enough to significantly increase whale populations. In 1986, the International Whaling Commission placed a moratorium on commercial whaling, which was largely successful, although it did not eliminate subsistence whaling or so-called 'scientific' whaling. This moratorium has led to significant recovery of some species, but its impact going forward may be limited since Japan withdrew from the commission in 2019.

Data on whale populations prior to 1986 is scarce, but there is a small amount of useful, if incomplete, information from whale catch data. Some species experienced sharp increases in hunting followed by sharp decreases, while others experienced gradual increases followed by sharp decreases [2]. Most whale populations remain severely depleted, but there are isolated examples of significant recovery.

1. Estimates based on mathematical modeling suggest that the historical population of New Zealand right whales was somewhere between 29,000 and 47,000. Hunting in the 19th century depleted the population to a mere 120 by the beginning of the 20th century. The current population estimate of about 2,200 shows that the population is recovering, but still dangerously low [5].

2. Annual catches of humpback whales in the west South Atlantic breeding group peaked at about 12,000 in 1910 before falling sharply to 2,000 in 1913. Modeling

estimates suggest that the population dropped below 1,000 by about 1915 and stayed at that level for several decades. Increased hunting in 1950 reduced the population in a single year to near extinction. A slow recovery began in the 1970s with accelerating growth after the International Whaling Commission's 1986 moratorium. Data from 2008 and 2012 showed a population approaching 20,000 [10].

Because there is no clear data on whale populations during the population declines, we focus here on using a model to explain qualitative features that are at least consistent with the limited historical record. In particular, it seems likely that there are populations that experienced a rapid decline while being subjected to only a modest increase in hunting and have remained depressed in spite of conservation efforts. This scenario is what we will explain with our model.

We begin by developing a resource management model in Section 2. We scale the model in Section 3 and analyze it in Section 4. The association of the model with the context of our whale population scenario appears in Section 5, followed by a discussion of further work and options for teaching the model in Section 6. All of these topics will be at least somewhat novel for most mathematicians. The model we present in Section 2 is similar to standard models for predator-prey dynamics, but the Holling type 3 component is largely unknown outside of the mathematical ecology community. Preparation for analysis by scaling does not appear in any currently available differential equations book as far as I know, although it does appear in a mathematical biology book [6]. Even the phase-line analysis in Section 4 will be novel to nearly all readers, as it is based on recasting the differential equation using a structure that greatly simplifies the analysis.

2 Derivation of A Resource Management Model

Mathematical models for predator-prey systems and consumer-resource systems are identical. While the predator-prey terminology is more common, the consumer-resource terminology is more appropriate in the context of resource management. Hence, we begin with a system consisting of a dynamic resource level $X(T) \geq 0$ and a dynamic consumer level $Y(T) \geq 0$, where T is time.[1] The dynamic variables are usually thought of as population sizes, but in many cases it is more biologically correct to think of them as biomasses [3], the idea being that predators will eat two half-grown fish as a substitute for one full-grown fish. Thus, we think of X as the biomass of a resource (whales) and Y as representing consumers (people) in terms of units based on the total potential consumption (so that two half-size fishing boats are equivalent to one full-size boat). In its most general form, we have the system

$$\frac{dX}{dT} = G(X) - YH(X), \tag{2.1}$$

$$\frac{dY}{dT} = EYH(X) - MY. \tag{2.2}$$

In this formulation, $G(X)$ represents the growth rate of the resource in the absence of consumers and $H(X)$, known to biologists as the 'functional response', represents the

[1] The reason for using T rather than t for time will become apparent in Section 3.

harvesting rate per unit of consumers at a given resource level. The parameter $M > 0$ is the natural decay rate constant of consumer units over time, while the parameter $E > 0$ is an efficiency of conversion from total harvested resource amount to units of consumers. Various growth and harvesting functions can be chosen, subject to reasonable restrictions. We assume that there is no growth when the resource level is 0 but that there is positive growth for resource levels sufficiently small; thus, $G(0) = 0$ and $G'(0) > 0$. The harvesting rate should be an increasing function of resource level, but 0 if there is no resource; thus, $H(0) = 0$ and $H' \geq 0$.

The simplest and most common example of a consumer-resource model is the Lotka-Volterra model, obtained by choosing linear functions $G(X) = RX$ and $H(X) = SX$. This widely used model is actually a very poor choice for predator-prey or consumer-resource interactions (see Section 6.3), so we will instead develop our own choices based on plausible biological assumptions.

2.1 Growth and Harvesting Functions

The natural choice for a growth function is

$$G(X) = RX\left(1 - \frac{X}{K}\right), \tag{2.3}$$

which prescribes logistic growth with maximum rate R and carrying capacity K. Our resource will then exhibit logistic growth in the absence of consumers.

The obvious choice for the harvesting function $H(X)$ is the linear function $H(X) = SX$, which is used in the Lotka-Volterra model and a number of other models. It seems reasonable at first thought that the harvesting rate per consumer should be proportional to the resource population. However, this model predicts that there is no limit to how large the harvesting rate can be. Clearly if the resource level is enormous, a consumer can only harvest so much. If you catch a fish every time you cast your line into the water, then you will spend nearly all of your time reeling in the fish, taking it off the hook, storing it, and preparing for your next attempt. Increasing the number of fish in the lake beyond this point is not going to help you catch fish faster. This saturation effect had been observed in predation data, but it remained empirical until given a mechanistic derivation in the 1950s by C.S. Holling [4]. Ecologists today associate Holling's name with a collection of three related functional response models, starting with the linear model, known as *Holling type 1*. Because the choice between the three models is critical, we present here the derivation of the Holling type 2 and type 3 models.

The key insight needed for the mechanistic derivation of both the Holling type 2 and type 3 models is that consumers must divide their time between searching and processing. Harvesting of a resource only occurs during time spent searching, so if the resource discovery rate is SX and T_s is the fraction of time spent searching, then the total harvest rate per unit time is

$$H(X) = T_s SX. \tag{2.4}$$

If we assume all harvesting time is spent searching, then $T_s = 1$, and we get the linear model. If some time is spent processing the harvest, then the fraction of time spent in searching is dependent on the harvest rate, which means that we need another equation to supplement (2.4).

Assume that each unit of harvest requires processing time B. Since consumption occurs at the rate H units per total time, the associated processing time is BH. One unit of total time is then partitioned between processing time and searching time; thus,

$$T_s + BH = 1. \tag{2.5}$$

Combining (2.4) with (2.5) yields the Holling type 2 model

$$H(X) = \frac{SX}{1 + BSX}. \tag{2.6}$$

As written, the model uses the biological parameters S and B. These are very difficult to measure, so it is more common to do experiments to measure values of H for various X. The model can then be parameterized from data, for which purpose it is best to rewrite it in terms of empirical parameters. If we define $Q = 1/B$ and $A = 1/BS$, the model takes the form

$$H(X) = \frac{QX}{A + X}, \tag{2.7}$$

where Q is the asymptotic limit of consumption per consumer unit and A is the level of resource for which consumption will be half of the maximum. This is the more common form of the Holling type 2 model.

Most ecological models use either Holling type 1 or type 2. The simplicity of the linear type 1 model makes it preferable for any biological system in which resources are scarce and consumers really do spend most of their time searching rather than processing. Such systems are relatively uncommon, as it is hard for organisms to survive if food is so scarce that they are almost constantly looking for it. Thus, the type 2 model is the one that is usually used in theoretical ecology. However, there is still a problem with the type 2 model that deserves attention. It is appropriate for specialist consumers, who are reliant on one specific resource. Generalist consumers have other options; as an example, bears eat a variety of foods and will decrease the amount of effort they put into fishing during periods when fish are scarce. The Holling type 3 model is designed for cases such as this. Instead of using a search rate S that is independent of the availability of the resource, suppose we make the search rate proportional to the resource level, with maximum rate S for a resource level at the carrying capacity K. This assumption roughly corresponds to the idea that the consumer is dividing its time between different resources and will do more searching for a plentiful resource than a scarce one. Replacing S with SX/K in the type 2 mechanistic model (2.6) yields the mechanistic version of the type 3 model:

$$H(X) = \frac{SX^2}{K + BSX^2}. \tag{2.8}$$

As with type 2, it is common to write the model using empirical parameters that can be determined from data rather than biological parameters that are hard to measure. With new parameters defined by $Q = 1/B$ and $A^2 = K/BS$, we obtain the graphical version,

$$H(X) = \frac{QX^2}{A^2 + X^2}. \tag{2.9}$$

The left panel in Figure 1 compares the graphical versions of the Holling type 2 and type 3 models. The type 3 model is initially concave up for small resource levels, which leads to different long-term behavior than would be the case with Holling type 2.

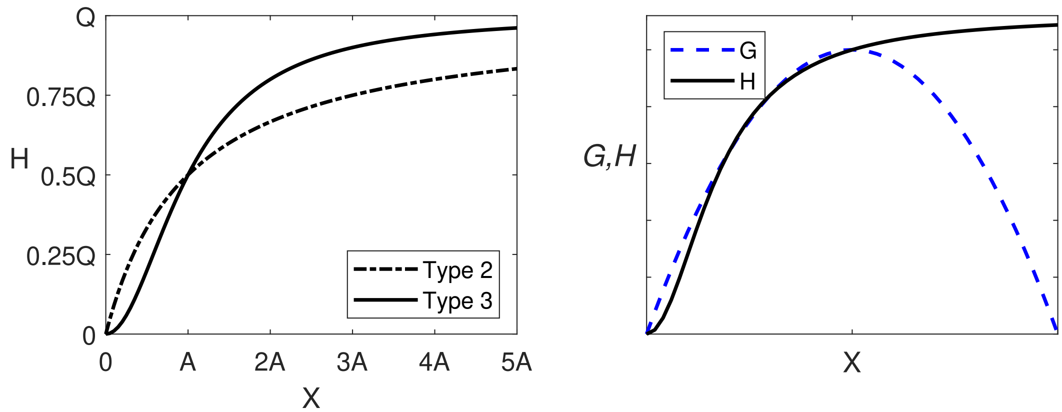

Figure 1: Left: The Holling type 2 and 3 functional responses. Right: A comparison of logistic growth and Holling type 3 harvesting functions. With the given parameter values, the G and H curves cross at three points, resulting in different system behaviors for different ranges of X.

2.2 The Resource Management Model

As presented in the usual way (Equations 2.1–2.2), we have a dynamical system of two interacting populations. The consumer level responds to changes in the resource level because harvesting leads to growth in the consumer population. But suppose the consumers are not a biological population, but rather a community of harvesters within a population, such as the community of fishermen within a human population. Then it makes sense to think of the number of harvesters as a parameter determined by public policy rather than a population whose size is determined by population growth. The result is a modified prey equation, with the dynamic variable Y replaced by a parameter $C \geq 0$. In this sense, the model maps the parameter C to a 1-variable dynamical system for X, suggesting questions about how the behavior of that system with given functions G and H depends on the parameter.

Using the mechanistic version of the Holling type 3 model, we obtain the complete resource management model

$$\frac{dX}{dT} = RX\left(1 - \frac{X}{K}\right) - C\frac{SX^2}{K + BSX^2}. \tag{2.10}$$

It would make sense to use the graphical version if we had empirical data to help determine Q and A. The mechanistic model is preferable here because it facilitates biological interpretation.

Although our model is merely a one-dimensional dynamical system, it is capable of rich behavior. This is suggested by the right panel of Figure 1, which compares the growth and harvesting functions, with parameters carefully chosen to indicate that the location of points where $G = H$ can be very sensitive to the parameter values in the functions.

3 Scaling

Model (2.10) has five parameters (although it could be thought of as having just 4 parameters by using CS and BS instead of C, B, and S). This is not an issue if our interest is limited to studying the model with one or two sets of known parameter values, but it is far from ideal if our goal is to characterize the full range of model behaviors. We can address this issue by scaling the model; that is, by replacing the dimensional variables X and T with dimensionless counterparts that are ratios of the dimensional quantities to carefully chosen representative values. Scaling is ubiquitous in some areas of mathematical modeling, such as fluid mechanics, while being relatively uncommon in population dynamics. This is in part because the choices of scales and dimensionless parameters in population dynamics are subtle (see [6] for a gentle introduction to scaling in population dynamics and [7] for a more thorough guide).

The choice of scales for a model is often tricky, but this is not the case here. We are thinking of scenarios in which the consumption parameters C, S, and B change gradually over time, so it is best to use scales that come from the growth term rather than the harvesting term. This means we should choose K for the reference resource level and $1/R$ for the reference time.

While scaling is usually thought of as a process of constructing new dimensionless variables, I find it helpful to think about it as a process of factoring a dimensional variable into the product of an appropriate dimensional constant and a dimensionless magnitude. Several notation conventions are in use for connecting dimensional variables to their dimensionless counterparts; I find the simplest to be upper case Latin letters for dimensional quantities and lower case Latin letters for dimensionless ones. The minor inconvenience of using T for dimensional time adds far less confusion than the corresponding inconveniences of other notational systems. Thus, we factor the variables X and T in terms of scale factors K and $1/R$ and dimensionless variables x and t as

$$X = Kx, \qquad T = R^{-1}t. \tag{3.1}$$

Making these substitutions and rearranging factors yields

$$x' = x\,(1 - x) - \frac{CS}{R}\,\frac{x^2}{1 + BSKx^2},$$

with the prime symbol indicating the derivative with respect to dimensionless time.

Notice that the five dimensional parameters have naturally sorted themselves into two dimensionless groupings, allowing us to rewrite the model in terms of two dimensionless parameters. There are multiple ways to do this [7], and the best choice is often clear only after doing the analysis. Our choice here is to factor BSK out of the denominator to get

$$x' = x\,(1 - x) - \frac{cx^2}{p + x^2}, \qquad p = \frac{1}{BSK}, \quad c = \frac{C}{BRK}. \tag{3.2}$$

It is helpful to examine the specific dimensionless parameters to identify a biological interpretation. The quantity $1/B$ is the rate at which a harvested resource can be processed, while the quantity SK is the rate of resource discovery when the resource is at its carrying capacity; thus, the parameter p can be interpreted as the 'processing to discovery' ratio. We will focus on small values of this ratio, corresponding to large natural populations. The maximum growth rate of the resource is $RK/2$, which is enough production to fully support $BRK/2$ units of consumers, given that each consumer requires B units of time to process one unit of resource. A value $c = 0.5$ therefore means that the maximum productivity is just adequate to support the number of consumers present. Clearly values of c at or above 0.5 will deplete the resource. Of course the actual results will be more subtle than this, but it is helpful to have some sense of what to expect prior to doing the analysis.

4 Analysis

The first step in an analysis plan for modeling is deciding what questions to address. It helps to think of a model as a mapping from the parameter space to some desired outcome. In dynamical system modeling, we typically look for stable equilibrium solutions and their domains of attraction. Our model has two parameters, one that represents the consumption effort (c) and one that combines the biological characteristics of the growth and hunting processes (p). Over the course of historical time, search speed has increased while handling time has decreased. These trends tend to result in less long-term change in the product SB that appears in the definition of p. It is therefore not unreasonable to assume that a particular whale community will have some fixed value of p, but that these will differ among species and regions. We therefore ask the following question:

- For any given value of p, how does the pattern of stable and unstable equilibria depend on the parameter c?

As a case study for students, more that one variable parameter means there is too much detail; hence, we assume a specific value $p = 0.01$. This value is chosen in hindsight because it is in the range where the most interesting behavior occurs. The influence of p is addressed in Section 6.

There are four types of analysis that we could consider doing with a continuous dynamical system: finding an analytical solution, using the phase-line to determine equilibria and stability, using linearized stability analysis to determine stability, and running simulations. Linearized stability analysis is not as good as phase-line analysis, both because it is more work and because phase-line analysis yields global as well as local stability. Simulations can be run using any numerical differential equation solver, but one can only do examples rather than general cases. This is warranted when trying to match a real data set. These considerations suggest we focus on finding an analytical solution and doing phase-line analysis.

4.1 An Implicit Solution Formula

Textbooks often emphasize analytical solution methods. While such methods have their place, it is easy to be misled by the emphasis placed on them into thinking that they have value for a large class of problems. Our model (3.2) is first-order and autonomous, which means that it can be solved by separation of variables. However, the solution has to be expressed implicitly using a definite integral:

$$t = \int_{x(0)}^{x} \frac{(p+y^2)\,dy}{y[1-(c+p)y+y^2-y^3]}. \tag{4.1}$$

This solution has no practical value, whether for our current investigation or a different one. Using it to determine long-term behavior of solutions would require identifying the range of upper bounds (both less than and greater than $x(0)$) for which the integral converges, which is a daunting problem. Given an initial condition and parameter values, we could plot graphs of the solution by identifying the time corresponding to any particular x; however, this requires a numerical method to compute the integral for each point, along with additional code to make sure the particular x chosen for a given point is one for which the integral converges. It requires far less numerical work to use a numerical differential equation solver on the initial value problem.

4.2 The Phase-line

The idea of phase-line analysis is simple: plot a graph that can be used to break the x axis into regions where x is increasing and regions where it is decreasing, then use this information to plot an x axis with arrows showing which equilibria are stable and which are unstable. The naive way to do this is to use a graph of x' vs x to determine when x is increasing. This method appears in nearly all differential equations books written since the initiation of the calculus reform movement around 1990. In the case of our model, the graph of the function

$$x\,(1-x) - \frac{cx^2}{p+x^2}$$

depends on the parameters p and c in complicated ways. Even with a single fixed value of p, the analysis is entirely procedural because we can only obtain the graph for specific values of c.

As an alternative to the naive approach, we can use an approach that preserves our intuition by imposing a structure on the function in the differential equation. The plan is to write the formula for x' using the structure

$$x' = f(x)[g(x)-h(x)], \qquad f(0)=0, \quad f'>0, \tag{4.2}$$

where fg is the growth rate and fh is the harvesting rate. These requirements do not yield a unique factorization; for example, we could choose

$$x' = x\left[(1-x) - \frac{cx}{p+x^2}\right] \tag{4.3}$$

or

$$x' = \frac{x}{p + x^2} \left[(1 - x)(p + x^2) - cx \right]. \tag{4.4}$$

Before choosing which factorization to use, it helps to understand how the functions f, g, and h will be used. For any factorization (4.2), we may draw the following conclusions:

1. $x = 0$ is an equilibrium point for the differential equation.
2. All equilibria other than $x = 0$ are points where the graphs of g and h intersect.
3. The state variable x is increasing whenever the graph of g is above the graph of h and decreasing whenever the graph of g is below that of h.

If possible, the choice of factoring should be made so that the graphs of g and h can be sketched by hand. Neither of the options works for both g and h, but option (4.4) is more attractive because our principal parameter c appears only in the simpler function. For any fixed p, the nonlinear function g needs to be graphed just once and we can superimpose multiple plots of the linear function h.

4.3 Phase-line Analysis of the Resource Model

The top left plot of Figure 2 shows the graph of the nonlinear function $g(x)$ with $p = 0.01$ along with lines of three different slopes. While the graphs of g and h are not the growth and harvesting functions, they nevertheless *represent* these functions in a relative sense, that being given by conclusion 3 above.

When $c = 0.12$, there is one positive equilibrium, at a value not much less than the environmental capacity 1. This equilibrium is identified by the intersection of the curve and the line and marked as a disk on the x axis. The point $x = 0$ is also marked as an equilibrium because this is built into the structure (4.2). For populations between these two equilibrium values, the curve g is above the line h. This means that growth outstrips consumption and the population increases, as marked by the arrow pointing to the right. To the right of the positive equilibrium, the graphs are reversed, so the population decreases. The arrows show that the positive equilibrium is globally asymptotically stable, while the extinction equilibrium is unstable. Given $p = 0.01$, the specific case $c = 0.12$ is representative of a range of 'small' values of c. Consumption is relatively low and the stable equilibrium population is relatively high.

When $c = 0.36$, as seen in the lower right panel, the situation is similar, except that the consumption level is sufficiently large that the single positive equilibrium is at a very small value of the resource. It is still true that the curve is above the line for values of x between the two equilibria and below the line when x is to the right of the positive equilibrium. As before, the positive equilibrium is globally asymptotically stable, and the extinction equilibrium is unstable. The difference is that a moderate value, like $x = 0.4$, is now in the 'large x' region where the curve is below the line. The number of consumers is high, but the actual amount of consumption is not, since the consumption is given as fh and both f and h are small.

The lower left panel shows the more interesting case of an intermediate value of c. Here there are three positive equilibria, which partition the x axis into four regions. In

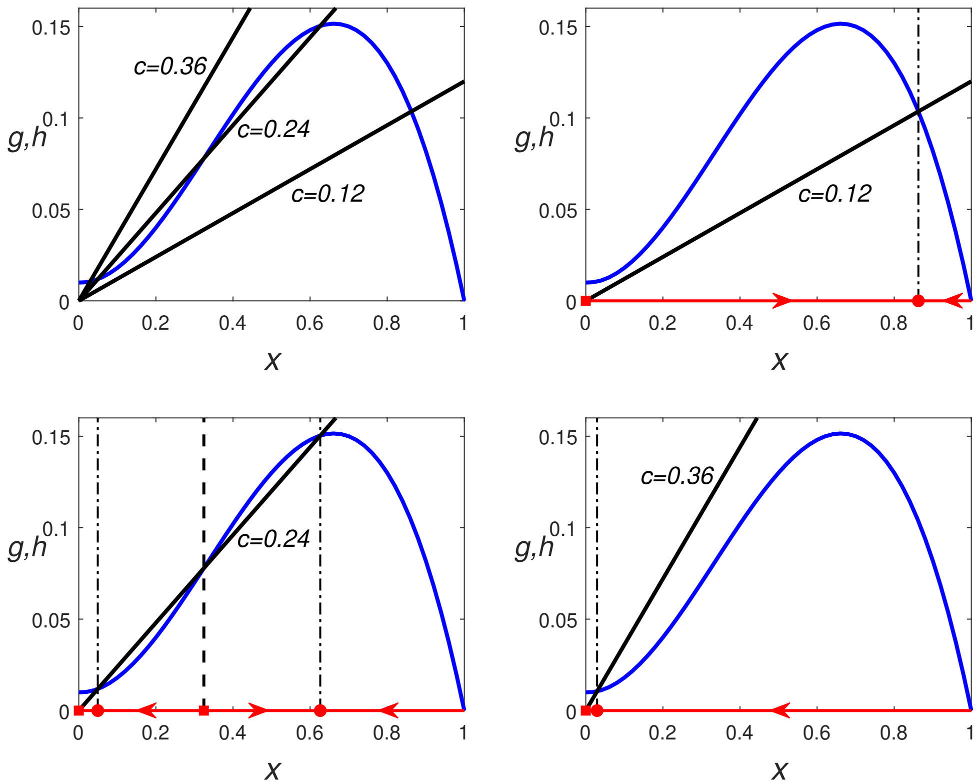

Figure 2: Plots of g and h from (4.4) with $p = 0.01$. Top Left: Three cases for c, showing a single large positive equilibrium for $c = 0.12$, three positive equilibria for $c = 0.24$, and a single small positive equilibrium for $c = 0.36$. The other panels show the cases individually, with the phase-line drawn on the x axis, using disks for stable equilibria, squares for unstable equilibria, and arrows showing the direction of change, which is always to the right when the curve (g) is above the line (h) and to the left otherwise. The unstable equilibrium at $x = 0$ is where $f = 0$.

the first and third of these, the curve is above the line, so growth exceeds consumption and the population increases. Similarly, the population decreases in the second and fourth regions because the curve is below the line. The result of this analysis is that the largest and smallest of the positive equilibria are locally asymptotically stable, while the middle one and the extinction equilibrium are unstable. The positive unstable equilibrium has special significance, as illustrated by the arrows: it marks the boundary between the domains of attraction of the two stable equilibria. Thus, the ultimate fate of the system depends on whether it starts above or below this critical value. This feature will play an important role in the application of these results to the history of resources that became depleted very quickly and have made only a modest recovery, such as some species of whales.

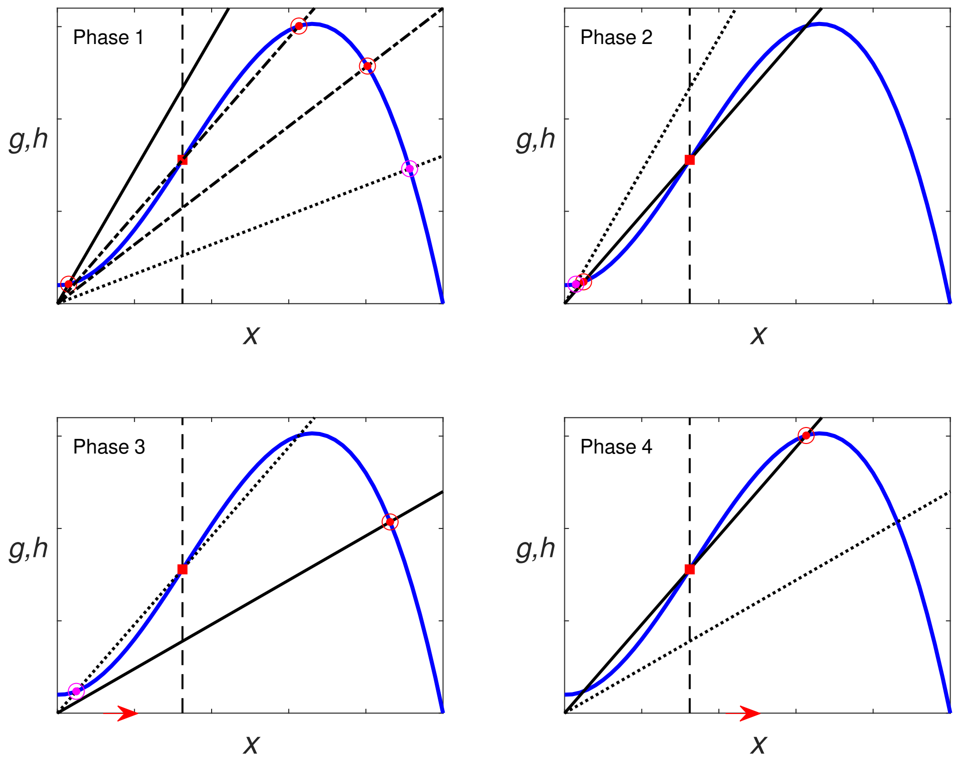

Figure 3: A reconstructed history of whale resource levels using $p = 0.01$. Each phase begins with a value of c corresponding to the dotted line and proceeds to the value of c corresponding to the solid line, with any intermediate values shown as dash-dot. The bulls-eye markers show the corresponding stable equilibria and the square markers show unstable positive equilibria. The arrows on the x axis in phases 3 and 4 indicate the direction of change toward a stable equilibrium.

5 A Reconstructed History of Whale Populations

Figure 3 shows a possible history of a resource that has suffered a sudden depletion and been difficult to restore. All phases assume $p = 0.01$; hence, the g curve is unchanged. The parameter c represents the capacity of humans to harvest whales rather than just the number of consumers. Thus, it increases naturally if unregulated, through a combination of human population growth and technological change. We assume that changes in c occur slowly enough that the system is able to continually adjust to the new stable equilibrium value, provided that equilibrium depends continuously on c. (This is not entirely realistic, as technological change can be sudden.) The history assumes that c increases naturally, represented by a steepening of the straight line, until some point at which it becomes controlled by public policy. Changes in population occur on two different time scales: both the increase in c and natural population growth occur on a scale of tens of years, while the depletion from unsustainable consumption can be much faster.

5.1 Phase 1: Depletion

Prior to the introduction of advanced technology, humans functioned as natural predators of whales. A small value of c, as indicated by the dotted line in the phase 1 plot, resulted in an equilibrium population only slightly below the environmental carrying capacity. Over a long period of time, the value of c rose steadily, gradually decreasing the equilibrium x, but slowly enough as to be unnoticeable over a human lifespan. Eventually, the value of c rose above the critical value that separates cases 1 and 2. At that point, seen in the second dash-dot line, there would have been two stable equilibria. The existence of a stable low-level equilibrium would have had no effect on the population, as the initial state for each successive consumption level would have been on the positive side of the unstable equilibrium. Only when c exceeded the critical value that separates cases 2 and 3 would there have been a drastic change. Once that critical value was exceeded, the high-level stable equilibrium disappeared, leaving only the heretofore unobserved low-level equilibrium. At that point, the initial condition was far from the final equilibrium value, so the decrease in population would have occurred on a time scale corresponding to the harvesting, whereas previously the population changes occurred on the much slower time scale corresponding to consumption increase. There is no question that some populations of whales, among other resources, have experienced a population crash at some point without a large contemporary change in consumption. This is different from instances where the consumption rate changed suddenly, such as the depletion of British forests during the rise of industry.

5.2 Phase 2: Inadequate Correction

Once a whale population became depleted, hunting them stopped being commercially viable. This would have caused a significant decrease in whale hunting efforts, which would have decreased the consumption capacity. Between that and the initiation of whale conservation efforts, c might perhaps have been lowered to the solid curve in the plot. By the solid curve, the system is back in case 2; unfortunately, this time the initial condition is at the prior low-level equilibrium, so it is the high-level equilibrium that is unachievable. As with phase 1, the phase 2 pattern is well documented for whales and other resources. This is what seems to have happened between 1961 and 1986, and it was difficult to sustain politically because the payoff was so low. Some stocks of whales are undoubtedly still in this phase, as not all have recovered as well as the west South Atlantic humpback and New Zealand right whales [9]

5.3 Phase 3: Strict Conservation and Restoration

As the environmental movement grew, international policy shifted toward further decreases in consumption, helped along by environmental activists such as Greenpeace. In phase 3, the decrease in c continues until the system is back in case 1. At that point, the low-level equilibrium is lost and the system begins to move toward the high-level equilibrium. Here again, the improvement in some whale populations is well documented and explainable using our simple model. Unfortunately, the time scale for restoration is much slower than the time scale for the depletion that occurred at the end of phase 1. In the depletion event, consumption outpaced population growth and drove the population decrease. In the restoration phase, the population increase occurs on the slower time scale of natural population growth.

5.4 Phase 4: Restoration and Sustainable Management

With a harvesting level corresponding to the solid line in the phase 3 plot and dotted line in the phase 4 plot, the whale population is recovering. If we maintain strict conservation for a while and then return to case 2, the outcome depends on whether the amount of restoration has raised the population above the unstable equilibrium value for the case 2 consumption rate. If so, as represented by the arrow on the x axis, we will have moved the population into the domain of attraction for the high-level equilibrium and the population will continue to grow in spite of an increase in consumption capacity. If not, we will still be in the domain of attraction for the low-level equilibrium and the population will begin to decline again. Of course the description of our current situation using the phase 3 and phase 4 plots is qualitative at best. We don't know the parameter values and there are flaws in the model that are not serious enough to falsify our narrative but are serious enough to make prediction uncertain. The prudent approach would be to maintain strict conservation until the population recovery rate is large and then increase consumption capacity only gradually. By monitoring the whale population and insisting on further growth, we can make sure that we have entered case 2 on the correct side of the unstable equilibrium. The point, though, is that it is not necessary to maintain strict conservation forever. A moderate consumption level that was not small enough for recovery in phase 3 is small enough for sustainability in phase 4. Based on recorded population data, we are clearly in phase 4 for some whale stocks [10].

6 Discussion

Here we consider a mathematical extension of the case study and turn to the practical question of how to teach the case study material in various ways.

6.1 Bifurcation Analysis

In our analysis of the model, we saw that the sensitivity of the equilibrium solutions to the parameter c is small at times and large at others, sometimes so large as to be discontinuous. The dependence of a solution on parameter values is of both mathematical and biological interest. It can be seen in a 1-parameter system by plotting a curve of the equilibrium value against the parameter. In a 2-parameter system, we can plot multiple such curves, using several different values for the second parameter. The left panel of Figure 4 shows such a plot for the model (3.2). The consumption parameter c is taken as the independent variable on the graph, while the process-to-discovery ratio parameter p is set at multiple values. The $p = 0.01$ case we have been studying is the second curve from the left and shows that case 2 requires c values roughly in the range 0.18 to 0.27. Plots of this sort are called bifurcation plots; the points where the stability changes on each of the three leftmost curves are called bifurcation points. The bull's-eye marker indicates what we might call a critical point, as it marks the critical value p^* that is the boundary between smaller p values, for which bifurcation occurs at some values of c, and larger p values that show no bifurcation in c. The plot shows that the corresponding value c^* also marks the largest value of c among bifurcation points.

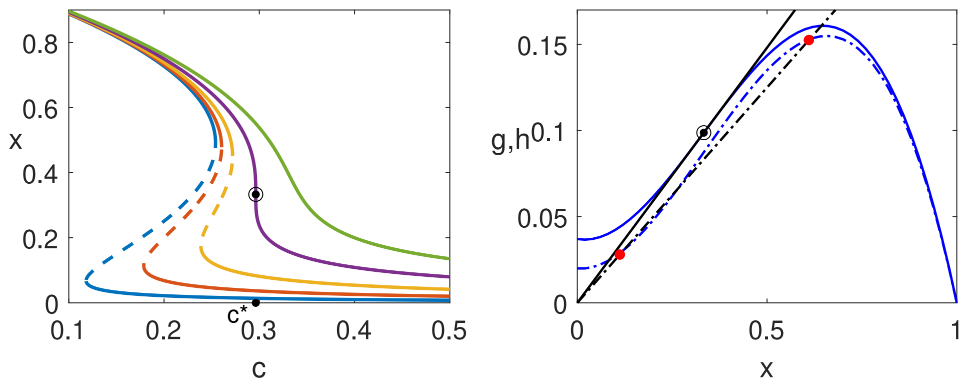

Figure 4: Left: Equilibrium resource levels as a function of consumer parameter, with p=0.004, 0.01, 0.02, 1/27, and 0.06, from left to right. Equilibria on the solid curves are stable, while those on the dashed curves are unstable. The critical value $p^* = 1/27$ is that for which the bifurcation curve has a vertical tangent, at the point with a bull's-eye marker. Right: multiple positive equilibria are possible if and only if $p < p^*$ and c is in a narrow range below c^*. The solid curve and solid line are for p^* and c^*. The dash-dot curve shows a smaller value of p and the dash-dot line shows a value $c < c^*$ corresponding to case 2, with disks marking the stable equilibria.

The critical parameter values can be determined analytically using a combination of calculus and algebra. The key to doing this is to identify the properties of the critical case on a plot of g and h from (4.2, 4.4), shown in the right panel of Figure 4. The solid line that marks the critical case is tangent to the graph of g at the inflection point, at the bull's-eye marker. The dash-dot curve in the plot shows that multiple equilbria occur for $p < p^*$, provided c is smaller than c^*, but not so much smaller as to be in case 3 of Figure 2.

The critical point is found by solving the set of equations for the properties that the critical case must satisfy, as seen in the right panel of Figure 4:

$$g(x^*) = h(x^*), \quad g'(x^*) = h'(x^*) = c^*, \quad g''(x^*) = 0. \tag{6.1}$$

Setting $g'' = 0$ yields the result $x^* = 1/3$. Then $g'(x^*) = c^*$ yields $c^* + p^* = 1/3$, and finally $g(x^*) = h(x^*)$ then yields $p^* = 1/27$. The discontinuous time histories of Section 5 only occur when natural resource stocks are large enough for the process-to-discovery parameter p to be sufficiently small.

6.2 Finding Equilibria

The plot on the left side of Figure 4 was obtained by solving the equilibrium relation for c and then computing the c values for a given set of x values. If we want to find the equilibrium points for a given set of parameters values, we need to solve the equation

$$(1-x)(p+x^2) = cx \tag{6.2}$$

numerically. Even with a professional root finder, such as Matlab's fzero function, this needs to be done carefully. Any solver works best when it is given a good approximate solution to start with, particularly when there are multiple solutions. The needed approximate solutions can be found graphically without much difficulty.

6.3 A Few Words About Modeling

A mathematical model is a collection of one or more variables together with enough mathematical equations to prescribe the values of those variables. Models are based on some actual or hypothetical real-world scenario and created in the hope that they will capture enough of the features of that scenario to be useful. This concept of models has an important consequence. The applications in most mathematics books begin with a listing of 'facts' used to derive the model. Given that models are based on, rather than equivalent to, a real scenario, what are given as 'facts' should be instead identified as *assumptions*, and the misleading term 'application' should be replaced by the more accurate term 'model.'

The distinction between applications and models is more than just nit-picking. One views mathematical results differently depending on whether the problem starts with facts or with assumptions. If it starts with facts, then the certainty of mathematics guarantees the certainty of the results, which must then be true statements about the scenario under study. If it starts with assumptions, then the certainty of mathematics guarantees only that the results follow from the assumptions, which means that their value in understanding the scenario is determined by non-mathematical considerations. In modeling, mathematical results need at least some degree of validation from outside of mathematics. At minimum, the qualitative behavior of the model should match the real scenario. As an example, the Lotka-Volterra model is the simplest instance of the broad class of predator-prey models (2.1–2.2), obtained with the linear functions $G(X) = RX$ and $H(X) = SX$. It predicts that no increase in the predator death rate is sufficient to drive the predator to extinction. This is sometimes stated as a biological outcome, when it is really only a mathematical outcome of a proposed model. Biologically, the result is clearly false in any realistic setting. The correct conclusion to draw is not that predators can't be driven to extinction, but that the Lotka-Volterra model is unsuitable for predator-prey modeling. That even this modest amount of validation is frequently overlooked is obvious from an examination of Google hits on 'Lotka-Volterra model': far more of these are for documents that use the Lotka-Volterra model to (incorrectly) 'explain' biological phenomena than for those that explain why the model should not be used.

Our model (3.2) has been derived from first principles and exhibits unusual qualitative behavior that matches a crude set of observed phenomena. This gives us some reason to believe that the story we tell about whales is plausible, but it should not be taken as a definitive explanation of real phenomena.

6.4 Using the Case Study in a Class

This case study can be used in several different ways, depending on the emphasis the instructor wants to place on modeling as compared to mathematics. We briefly outline several options, with increasing levels of modeling. The reader may also find it useful to have access to a Powerpoint presentation based on the case study [8].

Most differential equations courses today include phase-line analysis. This is always done by using graphs of x' vs x to determine whether x is increasing or not. It takes only a small amount of additional time to show the method based on the factorized form (4.2). The one-parameter equation

$$x' = x(1-x) - \frac{cx^2}{0.01 + x^2}$$

can be used as an example, with Figure 2 and the accompanying analysis. This can be cited as a resource management model without any of the modeling detail. A brief discussion of bifurcation could be included by using a plot of equilibrium x vs c, using just $p = 0.01$.

If an instructor wants to incorporate some modeling into the course, (s)he can present the two-parameter equation (3.2) with a brief statement that x is the resource level expressed as a fraction of carrying capacity, that time t is measured so that 1 unit of time is roughly the amount required for resource growth to be significant (rather than specifically time in days or years), that p is a parameter that represents the processing speed relative to discovery speed and will be small for large resource stocks because it is easy to discover things that are common, and that c is a parameter that represents the number of consumers, with $c = 0.5$ indicating a consumer level that would be sustainable only if maximum resource production could occur even with overutilization of the resource. This is the minimal amount of modeling needed to develop the historical analysis of Section 5. The students could be given the brief historical information in Section 2 or just the listing of articles cited in that section. The bifurcation analysis of Section 6.1 could be added to this option.

A full treatment of the modeling is suitable for courses that are as much focused on modeling as on differential equations, particularly courses based on projects or case studies rather than lists of topics. Such a treatment would include the derivation of the Holling type 3 model and the scaling, as well as all of the analysis. The bifurcation analysis would serve as an illustration of how modelers should try to extract as much understanding as possible from a model, and that this depends on doing a variety of experiments and asking questions about the results.

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