THE INFLUENCE OF CHAOS THEORY IN THE FIELD OF POPULATION BIOLOGY

NIB 3rd Semester Project
Roskilde University

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Abstract

This project seeks to find any influence that chaos theory had upon the field of population biology. For this reason, several papers, from 1974 up until the present day, were analysed with a view to obtaining an overall perspective of some of those influences. Two major factors were found; a better understanding of nonlinear systems and the rejection of the linearization of them, from this came a different view on the predictability of natural systems, in which it was found that accuracy diminishes with time, due to the fundamental characteristics of nonlinear systems, attributed to a sensitivity on the initial conditions.

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1.Introduction

It is the job of the physicist, not the mathematician, to extract and discover the set of natural laws and rules that govern the external world. For example, distances in space between two points can be calculated using Euclidean geometry, however, close to the speed of light, we must use a different set of rules, a different type of Geometry (Ekeland 1998). This does not necessarily mean that the rules of Euclidean geometry are any less true, even if reality refuses to conform. Chaos theory, much like Euclidean geometry, is a set of mathematical statements independent of observed phenomena it is a necessary consequence of the modelling of time dependent, dynamical systems, a sensitivity to initial conditions and accordingly.

An approach is presented showing the development of chaos theory through mathematical modelling of populations in dynamical systems. The historical context is presented through several case papers as an outline of the most important developments surrounding chaos theory. A summation of each paper is provided with relevant arguments as to their pertinence and significance to chaos

This paper will convey the most important effects of the recognition of chaos through its influence upon population modelling, the discovery of extreme sensitivity to initial conditions and the consequent unpredictability of dynamical modelling in nonlinear systems which has changed the way in which standard modelling is to be considered. From the beginnings of linearization to the distinction between variability, noise and non-periodic chaos, the findings of chaos theory will be shown to be progressively more inclusive to the field, over the past 40 or so years through a series of case studies.

2. Research Question and Problem Area

How did chaos theory influence population biology?

In 1974 Robert May published an article in which he stated that chaos was ‘overlooked’ by linearization (May, 1974). Our hypothesis is that the development of chaos theory resulted in significant changes in population biology, mainly the standard linearization and its consequences. This project seeks to find out, if, after the evidence of chaos in nature, any significant changes appeared in population biology. For this purpose, several articles were considered, from 1974 up until the present.

This project's target group was ourselves before we started working on the project, thus with no prior knowledge about chaos theory. It is also aimed more generally at 3rd semester students of natural science and our supervisors.

2.1 A short history of Chaos

Chaos theory conjures up images of fractals, bifurcations, and water wheels; it is a theory that is well known but little understood. An early proponent of chaos theory from the 1880's was Henri Poincaré, while studying Newton's proposed three-body problem[1], he discovered that there existed orbits which were non-periodic and yet not forever increasing or approaching a fixed point (Wolfram, 2002).

This unpredictability was given a name in the 1960's and is what we now know as Chaos theory. The meteorologist Edward Lorenz, whose interest for chaos came accidently through his work with weather predictions created simulations of the weather using a set of differential equations on his computer. His model showed a very high sensitivity to the initial conditions, as it turned out that rerunning the same simulation with the same initial settings produced drastically different results each time. Although the paper was published in a little known journal its significance remained unrecognised for a long time.

The first scientific paper to expose the existence of chaos in nature was by the English scientist Robert May in 1974. Robert May had a physics background and was familiar with mathematical modelling techniques which were not so familiar to Biologists. By demonstrating that chaos was present in simple models of population, May was successful in showing that random behaviour occurred even when the initial equations were known. (May, 1974). The paper turned out to be seminal and was the beginning of the application of chaos theory to the field of population biology. Although it took over a decade for anybody to really acknowledge the presence of chaos in population biology, (Gilpin, 1984) its application proved to be successful at improving predictions, yielding more accurate results in population modelling as well as other scientific fields (Li et al. 2013).

3.Theory

In this section, we will explore the general theory of chaos using real world examples, this will provide an overview and general outline of what chaos is. The succeeding part will delve more deeply into the characterising mathematics of chaos theory, the distinction between linearity and nonlinearity and the distinctions between chaos, noise, and variability. There are also some definitions of terms that the reader may be unfamiliar with, but will encounter throughout the paper.

The term chaos and chaos theory are somewhat interchangeable, the distinction being that the theory of chaos can be defined by several mathematical characteristics in which the behaviour of a dynamical system descends into chaos, the point at which predictability cedes.

[1] The three-body problem is a problem of taking a set of initial conditions of three particles or bodies (the moon, sun, and earth for example) and then determining the motion for them as they interact. Poincare could show that there was no general analytical solution for this problem as it was non-repeating (except in special cases). (Wolfram 2002)

3.1 Bifurcation

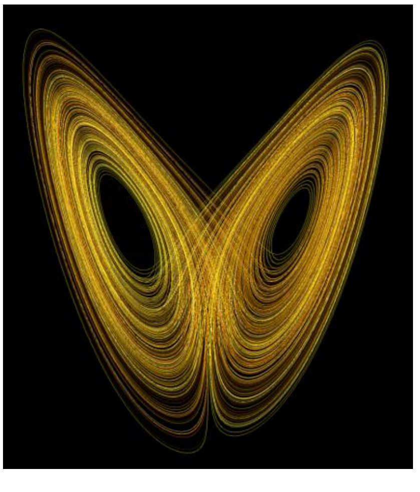
Bifurcation literally means the splitting of one body into two parts, for example; the forking of a river from its main body into two separate tributaries. It can also be seen in the structure of a tree root or the arteries of the circulatory system of a human body.

3.2 Attractors, strange and otherwise

Attractors are the set of states in phase space, invariant under the dynamics, towards which neighbouring states in a given basin of attraction asymptotically approach in the course of their dynamic evolution. In chaos theory, systems evolve towards states called attractors. The evolution towards specific states is governed by a set of initial conditions. An attractor is generated within the system itself. (Zeng, 1993)

There are several types of attractors. The first is the point attractor, for humans, this would-be death. The end is inevitable no matter what the path. the second is the limit cycle or periodic attractor where a system sets into a regular cycle through which it oscillates. Finally, the third type is called the strange attractor, it is chaotic and never repeats itself. The values will move towards a certain value, in the shape of a double spiral but the pattern never repeats itself. It is here that the significance of 3 variables appears most prominent. In 2D space the trajectory of a particle must cross its own, previous path when in motion around an attractor, to do so violates the condition of chaos by returning to a previous point. However, in 3D space a particle can escape this condition as it has a 3rd direction in which it can travel and 'avoid' the previous path. The double spiral shape of the strange attractor represents all the points in phase space occupied by all trajectories of the system. (Blesser, 2006)

Strange attractors have fractional dimension in that they are too detailed to be 2 dimensional, but too simple to be 3 dimensional. In this sense, they are fractals. They represent how details of a pattern change with scale, how it may grow in complexity as the scale changes, it can be thought of also, as an infinitely long line in a finite space. A fractal will scale differently to the space that it is embedded in. This is a difficult concept to understand and I hope it's a little clearer, there are many examples of how they can be visualised some of which are represented by nature in; the pulmonary system, dendrites of the nerves, tree roots etc. (Mandelbrot, 1967)



Left - The Lorenz strange attractor

The Lorenz strange attractor is a model based on 3 differential equations, in 3D space. Each component can be considered a separate species e.g. foxes, rabbits, grass. Each one's state is dependent upon the other 2 and the system generally tends towards a set of values as it evolves. Lorenz used this idea using the parameters of weather and the Oberbeck-Boussinesq approximation (a set of ODE's) to model, where he discovered what is now known as the strange attractor. Simply put, it is a butterfly pattern in 3d space where the trajectory of a particle never returns to the same space twice. Attractors come in other shapes, this is just the example of the Lorenz model. This is also an example of chaotic behaviour; the sensitivity of the initial conditions mean that any arbitrary starting point will never lead to the same trajectory twice. (Boeing, G. 2016)

3.3 The Double Pendulum (Levein 93')

In a dynamical system of more than two variables it is possible to witness chaotic behaviour, below is a description of the double pendulum, a dynamical system that exhibits chaotic behaviour.

The double pendulum system is a dynamical system of one pendulum attached to another. It is a simple physical design that exhibits rich, dynamical behaviour with a strong sensitivity to the initial conditions. Below is a graph of two identical, double pendulums (Fig. 1) alongside each other with their trajectories plotted out in red and blue. They start with the same initial conditions but quickly descend into different paths due to the sensitivity on these initial conditions. The pendulums both obey the same laws of physics but their behaviours progress in different manners, this is an inherent characteristic of chaos theory.

For a system to be chaotic it must be either nonlinear or infinite dimensional (Rosario, 2006). In the case of the double pendulum, with small motions (when the angles between the pendulums and the vertical axis are small, less than 1 radian) the system can be considered a linear system, by using the small angle approximation, we find that the system behaves like a harmonic oscillator and the nonlinear term(s) can be approximated by a linear term(s), (Boas, 2006). However, for large angles (greater than 1 radian), when we derive the equations of motion we find that the nonlinear terms cannot be so easily approximated and the system can become chaotic.

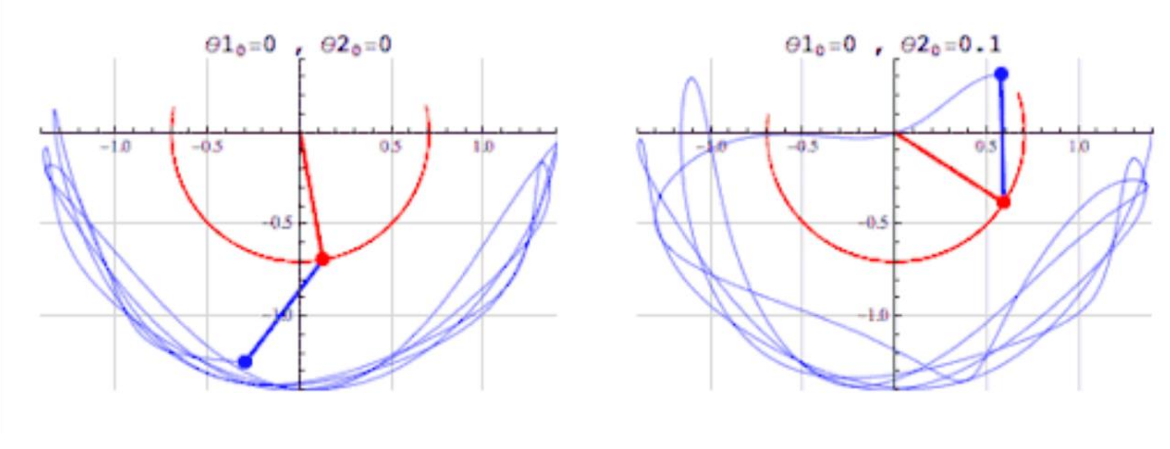


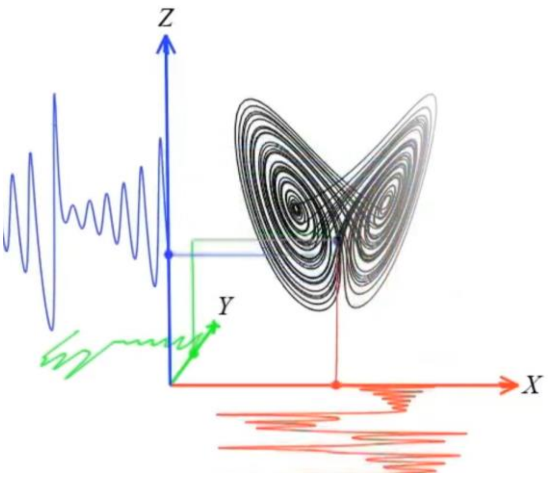
Fig 1. Double pendulum graph. Plot of trajectories in red and blue. Same initial conditions but different outcomes.[2]

[2] Taken from http://visualizingmath.tumblr.com/post/86258138836/chaos-and-the-double-pendulum
In the following link is a website with a computer simulation of the double pendulum with variables that can be manipulated. Also, the equations of motion are herein derived. http://www.myphysicslab.com/pendulum/double-pendulum/double-pendulum-en.html

3.4 Taken's Delay Embedding Theorem

Taken's delay embedding theorem is a method whereby the recreation of the behaviour of a chaotic dynamical system can be accomplished by manipulating (essentially time lagging) the data from the generic dynamical system.

Below you can see several graphs of a predator prey model. In this example, there are 3 variables; the variable x can be the grass, y the prey and z the predator. In a system of 3 or more variables it is possible to have chaotic behaviour. In this case the plotting of the relationship between these 3 variables creates a strange attractor in the form of a butterfly type shape. The first image below (figure 1.2) is a time projection from each axis creating a mapping of the behaviour of one variable in relation to the others. Using just one data set it is possible to create a time lagged projection and recreate the behaviour of the system with a degree of success (figure 1.3). Recombining two lagged versions of one time projected data set we can recreate something very like the original manifold. This newly generated manifold gives a one to one mapping between the original manifold and the shadow manifold (figure 1.4), this is known as cross mapping. Cross mapping allows us to estimate the states of the other two variables from the 3d space e.g. x from y or vice versa. Using the embedding theorem, it is also possible to determine causal relationships between the variables and subsequently improved selection of them. (Sugihara 2015).



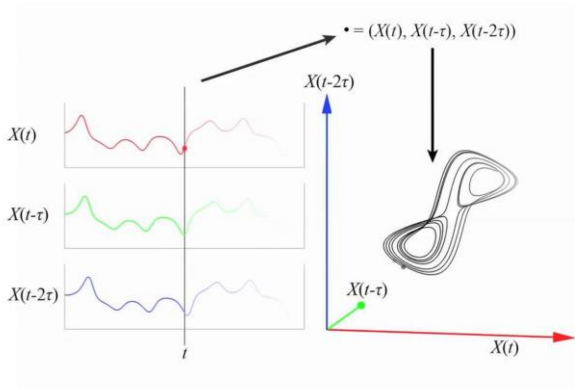
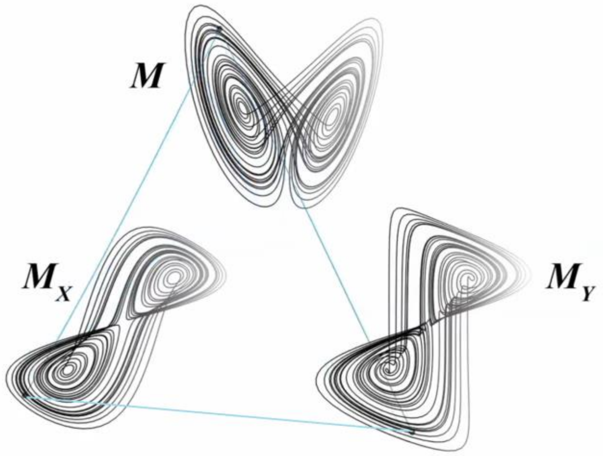


Figure 1.2 *above; a time series projection creates a strange attractor.*

Figure 1.3 *The recreated manifold with time lagged data.*

Figure 1.4*; bellow; Cross mapping manifolds.*



As the historical points of Mx are close to the historical points in My, it is possible to estimate the state of each variable from the other, a technique called 'cross mapping'. With longer time series, the mapping gets closer and more densely packed, increasing the accuracy of the predictions. This phenomenon is known as 'convergent cross mapping' and is helpful for predicting causation. (Sugihara 2015)

3.5 A note on noise and variability

Noise and variability were historically defined as when a system began to break down, this was interpreted as the system being no longer stable. This chaotic behaviour prompted scientists to spend years looking the other way, trying to reduce complex systems but rejecting ones that were chaotic. Robert May put it best when he spoke of 'the pedagogical importance of studying nonlinear systems to counter balance the often-misleading intuition fostered by linearity and traditional education.' (May 1984). We will discuss linearity a little more later.

3.6 Formal Definition of Linear and Nonlinear Systems

Before going into the characteristic of chaos theory, it would be pertinent to first make the distinction between linearity and nonlinearity. The following section aims to provide this detail.

Linear systems must verify two properties, superposition, and homogeneity. The principle of superposition states that the net response at a given place and time caused by two or more stimuli is the sum of the responses which would have been caused by each stimulus individually.

The principle of homogeneity simply states that the output of a system is directly proportional to its input. Homogeneity is implied from additivity for all rational, real, and continuous functions. Any function that does not satisfy superposition or homogeneity is nonlinear. It is worth noting that there is no unifying characteristic of nonlinear systems, except for not satisfying the two above-mentioned properties. (Hinrichsen 2005)

An example of a linear system is that of the equation for the straight line of a graph;

$$y = mc + x \qquad (1)$$

In this case, we know that this equation produces a straight line with an intercept at c and the gradient of the line determined by the value of m. We can see from our first definitions that this equation satisfies the conditions of being both additive and a scalar. It should be noted here that if x is the input then we don't have direct proportionality between input and output, and we don't have superposition. But if the input is a change in x, then we do. An example is given below;

If y=2x+3 then we can take x=3 and get y=9 but if we double x i.e. x=6 then we get y=15, which is not 18. So, in that sense the output is not directly proportional to the input. But if we take x=3 as some starting point (and y=9), then consider as our input a change in x of +1 i.e. we go to x=4, then the new y = 11 i.e. a change of 2. If our change in x was +2, (so x=5) then the new y would be y=13, i.e. a change of 4, which is twice the change we got from changing x by +1. So, in this sense it is proportional.

Nonlinear can also be more casually defined as the disproportionality of an output to an input. Thus, not satisfying the homogeneity property mentioned above. An example of a nonlinear equation would be

$$y = a + x^2 \qquad (2)$$

We can see from this that y would not be proportional to x due to the exponent.

3.7 Linearization

Also, known as linear approximation, linearization is the process of estimating a value. It is based on the tangent of a function near a given point. The tangent is describing the function best, for a certain point, as it goes in the same direction as the function. For the analytical function f(x), the following formula can provide a linearization of the function near the point a.

$$L(x) = f(x) - f'(x)(x - a)$$

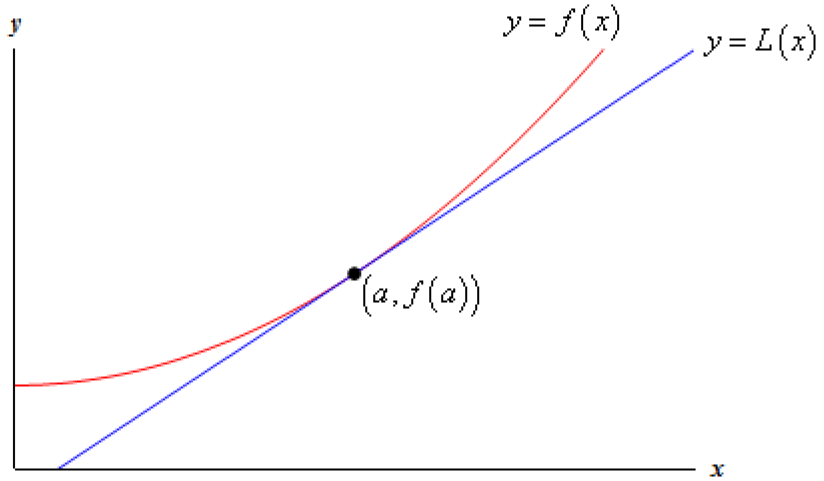


Figure 1.5: *Given a curve, as function y=f(x), the straight-line L(x) is drawn at the tangent taken from f(a). The points on the line L(x) are best approximating the values near the point a.*

In the case of the logistic growth equation, the former linearization cannot apply to the formula used in the logistic map section, as the equation is a discretized version of the function. Linearization can be applied in the case of a differential equation. The differential equation for logistic growth can be written as:

$$\frac{dN}{dt} = rN(1 - \frac{N}{K}) \qquad (3)$$

Eq. (3) has 2 stable points. One is when N=0, and the second one is when N=K. The stable points are the ones which, when the plugged in, the population tends towards equilibria.

The linearization equation for the logistic grow will take the following form:

$$\frac{dN(t)}{dt} = \frac{\partial r(N(t)(1-\frac{N(t)}{K})}{\partial N} * \Delta N(t) \qquad (4)$$

It can be observed that when derivation the logistic equation, the N^2 term is transformed in N. This transformation is the key to the problem faced when linearizing the nonlinear equations. Due to this, the rich dynamical behaviour is lost, and lead to the ‘overlooking’ of chaos.

3.8 Best fit line

In the case of an experiment, or a survey, lists of data are usually gathered. Aiding in calculations or predictions, that data can be fit usually in one type of function. For example, if the data seems to fit a linear pattern, a linear equation can be produced to describe the general behaviour. It is important to note that while linearization is a tool used in modelling of a function, the best fitting line, or regression line, is just a statistical tool to describe a specific set of data.

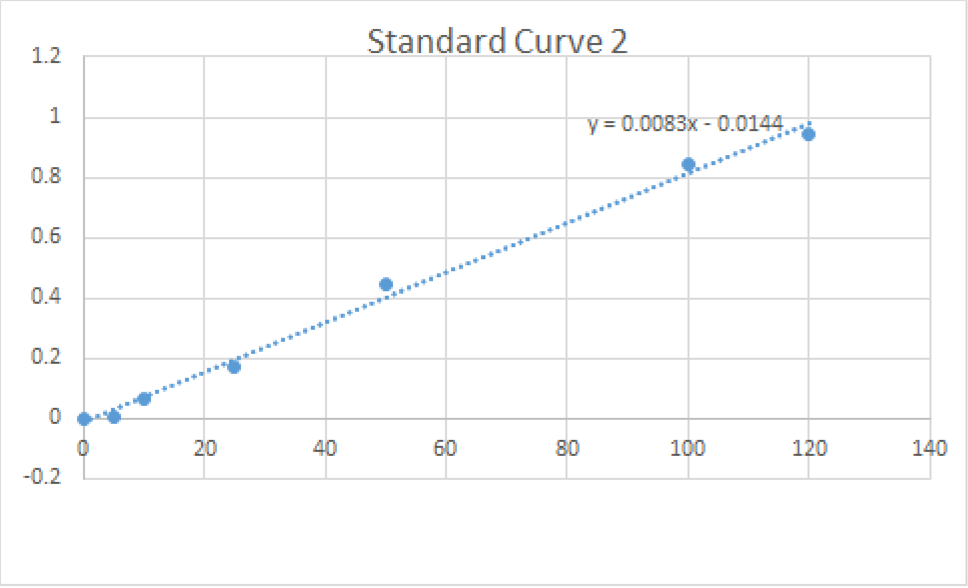


Figure 1.6: *Data from a gel filtration experiment of a mix of proteins, obtained in the course Biological Chemistry by Teodora Radut. The input data was fit into a line with the equation visible on the graph. This regression line aids further calculations for this data. As it can be seen, the line does not perfectly fit all the data as there are some points, above or below it, so it is not a perfect fit.*

3.9 Lyapunov exponent

A quantity that characterizes the rate of separation of infinitesimally close trajectories in a dynamical system. Quantitatively; two trajectories diverge with initial separation δz_0 diverge at a rate given by the following equation

$$|\delta Z(t)| \approx e^{\lambda t}|\delta Z_0| \qquad (5)$$

Were λ is the Lyapunov exponent. There is a spectrum of exponents, equal in number to the dimensionality of the phase space. The largest of which, the Maximal Lyapunov exponent (MLE), determines the predictability of a dynamical system and a positive value for this is usually interpreted as a chaotic system. (Boeing, 2016)

3.10 Modelling

Population modelling studies populations sizes, regarding matters such as reproduction, starvation, or even the effects of introducing another species into an ecosystem. Murray states that the size of a population usually fluctuates between certain values, which are often defined as the carrying capacity of one habitat[3] (Murray, 1979). The size of a population is also dependant on many factors such as: birth rate, interaction with other species, mortality rate, immigration, and emigration rates (Thieme, 2003). A special type of factor is found to have an importance in the population size, and those are the density-dependant factors; these include predation and disease, or competition for resources and are one of the regulating influences on the number of individuals in a population (Murray, 1979). They can explain, for example, why in some populations, after a period of exponential growth, the population clashes (Murray, 1979).

One example of a population model expresses the change in the population size, as a function of time (Thieme, 2003). A model of this type can predict the number of individuals in a population, and provide an estimation for the different effects that act upon it, for example how much does affect does a lower food supply have on the overall population[4].

The specific model we will focus on in this report is the logistic model which is based on the modelling of birth rate, and population from the previous year. Some of the cases that are discussed also consider the effects of several correlating populations and how they dynamically vary with each other. i.e. the predator-prey model.

3.10.1 The Logistic map

The logistic map will serve as a mathematical example of how chaos appears in natural systems. The logistic map is a recursive equation that demonstrates fluctuations of a population over a time series.

Firstly, we define the logistic equation (Eq.1 below). We can consider a simple theoretical population of insects. The model assumes there is only one population and does not include the effects of interference from any other population. We consider *xn* as the number of individuals in one year

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[3] [1] The carrying capacity of one habitat is the maximum number of individuals that can live in a certain habitat.

[4] Taken from An Introduction to Population Ecology - Introduction to Population Modelling | Mathematical Association of America," n.d.

(defined as the ratio of the existing population to the maximum population) and *xn+1* the number of individuals in the next year.

$$x_{n+1} = rx_n\,(1 - x_n) \qquad (6)$$

This model has distinct behaviour depending on the values of r.

1. If 0 < r < 1 xn tends to 0, meaning the population becomes extinct.
2. If 1 < r < 3 xn approaches a fixed value dependent upon a
3. If 3 < r < 3.56 xn does not approach a fixed value, it oscillates between 2 fixed points.
4. If r > 3.56 xn doesn't approach a fixed value or oscillate; the movement is chaotic.

This model becomes chaotic because of the sensitivity to the initial conditions, meaning in our case the sensitivity to r. It is important to realise here that no matter the number of individuals in one year, the number of individuals next year is dependent on the birth rate, and the population from the previous year. Below is a picture of the logistic map in which you can see the transition into chaos where the birth rate exceeds 3.56.

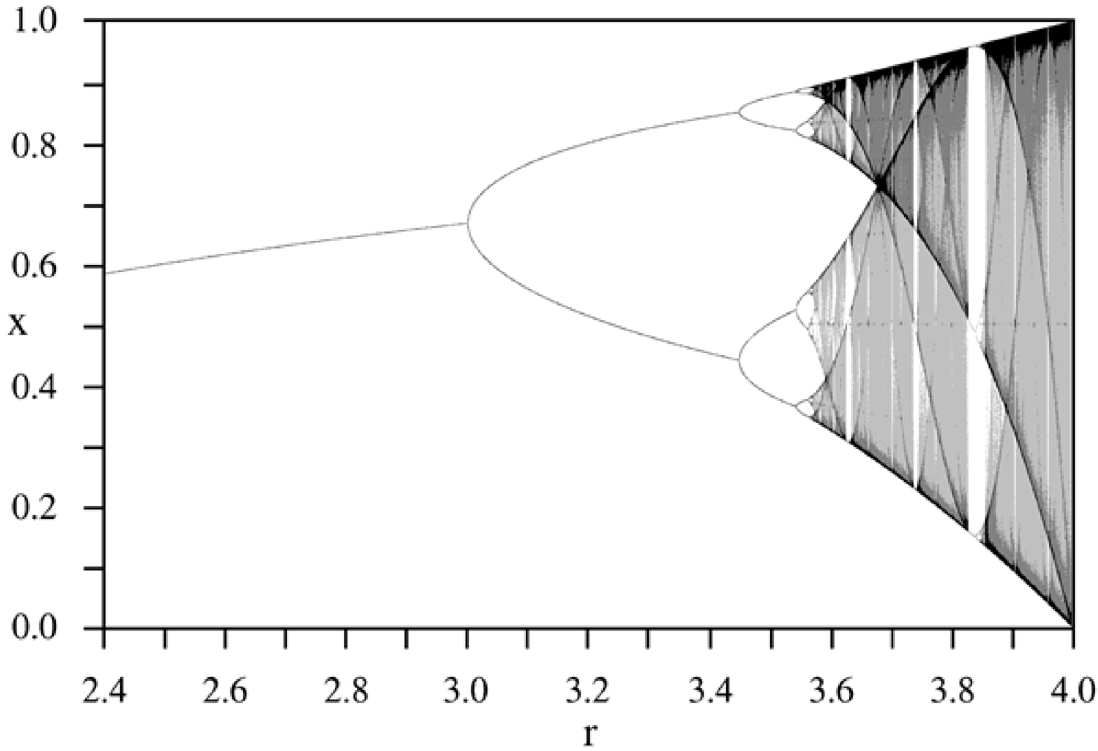

Fig. 2. Logistic map; *the mapping of the logistic growth equation; after an r value of 3.56, the chaotic state can be observed.*

3.10.2 The first Feigenbaum constant

As you approach chaos, each periodic region (defined by the point at which it bifurcates) is smaller than the previous by a factor approaching a number, this number is the first Feigenbaum constant. It is important because it is the same for any function or system that follows the period-doubling route to chaos. To show this mathematically we will use two examples, firstly a standard nonlinear equation. (Yorke et al. 1996)

$$f(x) = a - x^2 \qquad (7)$$

In this case *a* is the bifurcation parameter and *x* is the variable. The values for *a* at which the period doubles are tabulated below. We then define the Feigenbaum constant as the limiting ratio of the interval between each bifurcation, as it converges to the Feigenbaum constant from equation 8 below. Again, in this case *a* is the bifurcation parameter and delta is the Feigenbaum constant. a_n is the discrete value of *a* at the nth period doubling. Period doubling being where a system switches to a new behaviour with twice the period of the original system. (Yorke et al. 1996)

$$\delta = \lim_{n\to\infty} \left(\frac{a_{n-1} - a_{n-2}}{a_n - a_{n-1}}\right) \qquad (8)$$

As we can see in the table below (2.1), the value for delta converges at the first Feigenbaum constant with each successive doubling. This value holds for all functions that follow the period doubling route to chaos.

n	**Period**	**Bifurcation parameter (a_n)**	**Ratio $a_{n-1} - a_{n-2}/a_n - a_{n-1}$**
1	2	0.75	—
2	4	1.25	—
3	8	1.3680989	4.2337
4	16	1.3940462	4.5515
5	32	1.3996312	4.6458

6	64	1.4008286	4.6639
7	128	1.4010853	4.6682
8	256	1.4011402	4.6689

Table 2.1*; Nonlinear data set showing the convergence to the first Feigenbaum constant*

This behaviour is consistent for iterations of other, nonlinear sets such as the logistic map as we can see in the table below (2.2). A slight change in the systems parameter values (in the case of the logistic map this would-be *r*, the birth rate, (see Eq. 1) causes a bifurcation and the convergence of the successive ratios of this period doubling once again tends towards the Feigenbaum constant. (Yorke et al. 1996)

n	**Period**	**Bifurcation parameter (a_n)**	**Ratio $a_{n-1} - a_{n-2}/a_n - a_{n-1}$**
1	2	3	—
2	4	3.4494897	—
3	8	3.5440903	4.7514
4	16	3.5644073	4.6562
5	32	3.5687594	4.6683
6	64	3.5696916	4.6686
7	128	3.5698913	4.6692
8	256	3.5699340	4.6694

Table 2.2; *Logistic data set showing the convergence to the first Feigenbaum constant*

3.10.3 Model in MATLAB

The following section shows our work with some actual modelling of chaos, using scripts in MATLAB we could generate chaotic behaviour and analyse the transition between stable, periodic behaviour and Chaotic non-periodic behaviour. We began with the logistic map. Below (2.3) is a copy of the script and the graph generated from it.

```
% Logistics Map
clear
scale = 10000;
maxpoints = 100;
N = 2000; % "r" values simulatd
a = 1.0; % Starting value for "r"
b = 4; % Final value for "r"
rs = linspace(a,b,N); % "the r values"
q = 300; % number of repetitions of the logistic map

% Loop through the "r" values
for j = 1:length(rs)

    r=rs(j); % Current "r" value
    x=zeros(q,1);
    x(1) = 0.3; % Intial conditions between 0<x<1

    for i = 2:q, % iterate
        x(i) = r*x(i-1)*(1-x(i-1));
    end
    out{j} = unique(round(scale*x(end-maxpoints:end)));
end

% Rearranging the cell array for plotting n-by-2 for plotting
data = [];
for k = 1:length(rs)
    n = length(out{k});
    data = [data;  rs(k)*ones(n,1),out{k}];
end

% Plot the data
figure(97);clf
h=plot(data(:,1),data(:,2)/scale,'k.');
set(h,'markersize',1)
axis tight
set(gca,'units','normalized','position',[0 0 1 1])
set(gcf,'color','white')
```

Fig 3 Logistic map script in MATLAB

Most of the commands are explained in green above and next to each line of code. We created a plot also with an iteration up to a value of r = 4 by which time we have achieved chaos (Fig 3.1). We also created a graphic of an enlarged point at the transition into chaos illustrated in Figure 1.6 where the continual bifurcations become increasingly difficult to see but can just about be made out.

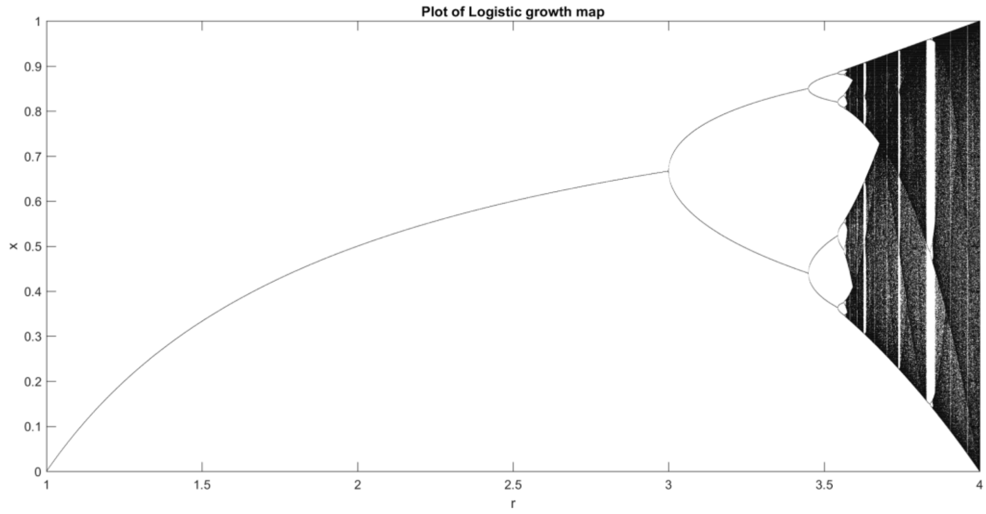

Fig. 3.1 Iterations of logistic map *in the figure above, it can be observed, the system's 'reaction' to the value of r. For a value below 4, simple bifurcation can be observed. For a value of 4, chaos can be observed.*

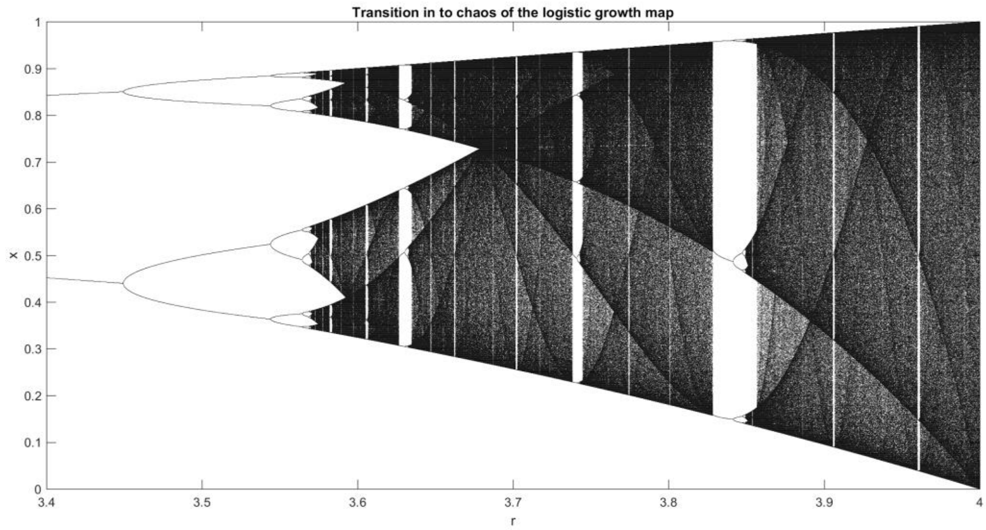

Fig. 3.2 Zoom on the logistic map. *In the figure above we can see an enlarged portion of the transition into chaos, the continuation of the bifurcations and period doubling with some big spaces were oscillations almost halts completely.*

Analysis

In the following section, we will summarise a series of cases that best reflect the influence and use of chaos theory in population modelling. The cases were selected per their relative accessibility, which year they were published (we want to give sense of progression over the last 4 decades) and how well they reflected the most significant aspects of chaos theory (sensitivity to initial conditions, short term prediction vs. long term and nonlinear dynamics).

The cases that are explored in the report, can be divided in 3 major categories; 1) The first cases that discovered chaotic behaviour in natural systems, 2) The cases that considered the intrinsic characteristics of nonlinearity in natural system, and 3) The cases that applied chaos theory in modelling. Presented for each article, are the H5 index, which is the largest number (h), for which at least the same number (h) of articles in that journal have been cited at least h times; and the citation number. For example, if one publication has an H5 index of 312, such as Science, it means that the journal has at least 312 articles that were cited 312 times.

The first cases that discovered chaos in natural systems

The seminal case by Robert May, in which he introduces chaos theory and its effect on modelling in population biology, was the first to apply the characteristic mathematics of chaos theory to population modelling. May paved the way for others as we will see later.

1. Biological Populations with Nonoverlapping Generations: Stable Points, Stable Cycles, and Chaos. May R. Science, vol. 186, issue 4164 (1974) (Cited by 1517 articles, H5 index for Science 312)

This was the first paper that explored the possibility of the existence of chaos in population modelling. Here, May succeeded in showing evidence of the existence of chaos in population modelling, often overlooked due to the convention of linearization. This exhibition of rich and dynamical behaviour, shown to be present in population models was not really acknowledged by ecologists until little over a decade later (Gilpin 1984). In 1989, it was shown to arise, theoretically, in almost any population model (Robert, 1989).

May takes a simple nonlinear equation and analyses it with a focus on the fluctuations of the birth rate, denoted with the same variable ‘r’ as in our previous examples. His purpose is to show that these types of equations (nonlinear equations) have been ‘*discussed inadequately, as having either a stable equilibrium point, or being unstable with growing oscillations*’ (May, 1974) when in fact as the rate r increases, the system is displaying behaviour from ‘*stable equilibrium point to stable cyclic oscillation between 2 population points to stable cycles with 4 points then 8 points and so on through a regime which can only be described as chaotic’*(May 1974).). Thus, they found oscillations between 2, 4,8 or more points, and then a chaotic state. In this paper, May had successfully proven that chaos was to be found in nonlinear equations, he had uncovered a rich dynamical behaviour which had been hidden by linearization.

This discovery has significant importance for population biology, as he states: '*For population biology in general (...) the implication is that even if the natural world was 100 percent predictable, the dynamics of populations with ''density dependent'' regulation could be nonetheless indistinguishable from chaos, if the intrinsic growth rate r is large enough'* (May 1974).

Showing that chaos can arise in simple models of population biology, this seminal article is the first one to propose that important dynamical behaviour is lost during linearization. Modelling in population biology now had to face a consideration that linearizing may not be such an accurate approach and that nonlinearity should be considered more thoroughly.

2. Nonlinear forecasting as a way of distinguishing chaos from measurement error in time series. Sugihara G May R. Nature, vol. 344, issue 6268 (1990) (Cited by 1534, H5 index for Nature, 359)

This article was published in 2 different journals, and for understanding the article fully, we shall regard both, one is focussed on explaining the method of May and Sugihara, while the second one, on their results. The general focus is that of creating a distinction between that of chaotic behaviour and errors in measurement (noise) in dynamical systems.

The first article investigates the importance and effect of environmental and biological factors, in terms of regulating the population size, while taking into consideration the system's nonlinear behaviour and the incorporating the idea that it could be chaotic. Starting from the premises that the environmental factors and the biological factors are '*often thought to*'(Sugihara & May, 1990) determine two different types of behaviour, the authors *'revise this idea in the light of recent work'*(Sugihara & May, 1990), and determine which factors are correlated with the specific behaviour. The authors then present a method of distinguishing between noise, and chaotic behaviour, which is applied to different data sets; measles, chickenpox, and marine plankton. It was in relation to this relative new theory in dynamics, concerning non-linearity and chaos that the authors divide the report into 4 major parts: first they present the shortcomings of traditional approaches in population dynamics, next they present their new method of distinguishing between noise and chaos; the third part consists of the application of this method to several data sets, and lastly their conclusions and future perspectives.

1) Limitations;
The authors exemplify one case in which (based on the old approach of linearizing) the data set would be characterised as having external influences, leading to a model with erratic results. They infer though, that this is not the case, as it is a simple model of chaotic behaviour. *'Yet these data do not we summarize as follows, represent density-vagueness at all, but are an example of simple chaotic dynamics that were generated from the deterministic tent map''* (Sugihara & May, 1990). Clearly here Sugihara and May claim to have found chaotic dynamics in a system long since disregarded as erratic. When regarding the limitation of the single factor approach-which is the regression of '*one explanatory variable against another*' they found that critical relationships are lost, appearing unrelated.
2) The new method;
By using Taken's embedding theorem, they can develop their approach. '(..)*we follow the short-term destiny of nearby points in the attractor to see where they end up after p time steps. This is a nonparametric method, and it should apply to any stationary or quasi-ergodic process, including*

chaos.' (Sugihara & May, 1990) From this quote we can see the beginnings of the application of Taken's embedding theorem and thus the beginnings of empirical dynamic modelling. Their method seeks to predict the trajectories of points nearby the attractor, which we will later see, is a method of determining the dynamics of the system.

3) Application of the method;
The data sets chosen are rather large, making it easier to detect patterns, this is because the chickenpox and measles cases are very well documented. When the new method is applied, the authors state that they could make short term predictions on the data that was presenting chaos, but not on the 'noisy' data. (*It is important to note that, when the article was published in Nature another time series was added, namely the marine plankton time series). Regarding their application of the method we shall consider the Nature article in more detail as it provides more information than the review. For the measles data set, the nonlinear predictions have a p value[5] of 0.0005, thus the predictions are optimal. In the case of the chickenpox time series, it is found the linear regression model has the same performance as the nonlinear model. The authors explain this, referring to several biological factors, such as the '*brief interval of infectiousness*'(Sugihara & May, 1990), and because of the legal differences in reporting the cases. In the case of measles, informing the relevant authorities was mandatory, which was not the same for chickenpox. For the last data set, the marine plankton time series, to quote the authors: '*significantly better fit of the nonlinear predictor, as compared with the optimal linear autoregressive model(P<0.0005)'* (Sugihara & May, 1990). Thus, a nonlinear model could predict more accurately than a linear regression model.
4) Conclusion and Future perspectives;
Sugihara and May conclude that their approach is feasible for the considered time series, and that this approach can be applied to other 'noisy' time series in population biology.

The article is thus demonstrating a new method in distinguishing between noise and chaotic behaviour. May and Sugihara apply their method to different data sets, and then analyse the forecast from both the autoregressive model and the nonlinear model, with more success coming from the new technique.

3. Spiral chaos in a predator-prey model – Gilpin, M. The American Naturalist, vol. 113, issue 2 (1979) (Cited by 299, The American Naturalist H5 index 45)

This rather short article, is further studying a predator prey model in which quasi-cyclic behaviour is found as stated in a previous paper (Vance, 1978) by a previous article. The important part of this report, is that the author is studying this trajectory of the predator prey population and classifies this specific type as spiral chaos. This paper is also important for their conclusion as they state: '*The message from this is that even the simplest possible models of community interaction require exhaustive cybernetic analysis before their repertoire of behaviours can be known, and some of these are likely to be complex. It is hardly any wonder that IBP-type models*[6]*, assembled from many nonlinear component models whose parameters are necessarily inaccurate and probably improperly lumped, have blown up, (...). The degree to which real ecosystem behaviour is chaotic is possibly the*

[5] The p value is the result of a statistical test, which gives the researcher an approximation of the probability of any of the results appearing in nature. A good p value depends, usually, on the research too, but any value below 0.05 is normally considered to be good, as it means the found results would match in 95% of the cases.

[6] IBP models are the models constructed during the International Biological Programme(IBP), which were meant to develop ecosystem models as a whole. (http://www.encyclopedia.com/earth-and-environment/ecology-and-environmentalism/environmental-studies/international-biological)

most fundamental question facing community ecology' (Gilpin, 1979). Thus, the authors are highlighting the rich dynamical behaviour than is found in their model, as well as the fact that nonlinear systems should be modelled accordingly.

In summary; this article is further investigating chaos in population models, and it can show that chaotic behaviour can be found in the simplest models, thus supporting May's claim from 1974. This is an example of further evidence that chaos is encounterable in population biology models, as far back as the late 70's.

4. Seasonality and period-doubling bifurcations in an epidemic model. Aron J Schwartz I. Journal of Theoretical Biology, vol. 110, issue 4 (1984) (Cited by 273, Journal of Theoretical Biology H5 index 44)

This paper is focusing on how seasonal variation is actually influencing an epidemic model, by describing '*a simple epidemic model with seasonal transmission and (we will) explore numerically its periodic solutions* '(Aron & Schwartz, 1984). The model divides the population into 4 categories: the people who can contract the disease, the susceptible (S); the people who have been infected, but are not infectious, the exposed (E); the people who can infect other people, the infective (I); and the last are the people who cannot contact the disease anymore, the recovered (R). Using the SEIR epidemic model, they can show that as the *'amplitude of the seasonal variation increases the solution may pass from a period 1 (annual) cycle to period 2 to period 4, etc., tending to a Feigenbaum transition to chaotic behaviour'* (Aron & Schwartz, 1984). The authors also emphasise the importance of more detailed studies to understand the interepidemic periods. As the papers before, this article is further evidence that chaotic behaviour is found in natural systems, in this case in an epidemic model. The exploration of chaos begins to further into more diverse fields.

5. Spatial structure and chaos in insect population dynamics. Hassell, M. Comins, H. May, R. Nature, vol. 353 (1991) (Cited by 844, Nature H5 index 359)

This article is regarding a mathematical model of host-parasitoid interaction. They consider that the environment '*consists of a square grid, containing many patches'*(Hassell, Comins, & May, 1991). In these patches they apply one equation to *'find how many hosts and parasitoid's will emerge in that patch in the next generation'*(Hassell et al., 1991). Then they are considering that some fractions of the hosts and parasitoid's are distributed in other patches. They are dispersing the individuals only in their neighbouring patches with an equal distribution. Their results are divided, as they can distinguish 3 patterns, among which is also chaos. To confirm their results by using cellular automaton; '*For a cellular automaton approach, we abandon detailed host and parasitoid population values, and acknowledge only these nine qualitative categories of patch densities. We then define a set of 'movement rules' that specify the colour of each patches next generation in relation to its present colour and the colour of its eight neighbours'*(Hassell et al., 1991).Thus in the cellular automaton method, the authors only consider the patch density, and they provide the rules for the insects to move from patch to patch. By using this they found the same 3 patterns, including one of chaotic behaviour. This article was also chosen due to its citation number and its publisher; Nature.

The cases that consider the intrinsic characteristics of nonlinearity in natural systems.

These are the articles which applied and included the idea of chaotic behaviour in ecosystems, and used it to understand the systems better.

6. Transition to spatiotemporal chaos can resolve the paradox of enrichment. Petrovskii S, Li B, Malchow H. Ecological Complexity, vol. 1, issue 1 (2004) (Cited by 99, Ecological complexity H5 index 21)

In 1971 Michael Rosenzweig coined the term ‘paradox of enrichment’, roughly defined as an effect in predator-prey models terminate their progression with a tendency to extinction for the predator. This occurs when the food for the prey is left unbounded, it destabilizes the population of the predator indirectly by allowing a proliferation of prey. (Rosenzweig, 1971). In the 2004 paper on spatiotemporal chaos, Petrovskii et al. demonstrate how, using two different models, a transition from stability into chaos can prevent species extinction in a predator prey model. This demonstration, acknowledging the presence of chaos, (which had also been shown in previous papers (Wave of Chaos, Petrovskii, 2000) enables a richer dynamical model to be produced. In regular dynamic modelling the predator would have tended to extinction thus validating the Rosenzweig paradox. A consideration of chaotic dynamics in the model enables a more realistic model to be produced.

7. Frequency dependence and viral diversity imply chaos in an HIV model. Iwami S, Nakaoka S, Takeuchi Y, Physica D: Nonlinear Phenomena, vol. 223, issue 2 (2006) (Cited by 6, Physica D: Nonlinear phenomena H5 index:33)

It is shown in this paper, that viral diversity and the frequency dependent proliferation of CTL’s[7] (T-cells that attack viruses) and elimination of infected cells in an immune system can produce strange attractors when the behaviour of two or more viruses are modelled. Considering an individual who is infected with HIV; the susceptibility of the body to viruses increases due to a weakened immune system, the proliferation of the diversity of these viruses and the frequency dependent behaviour of CTL’s which attack the infected cells is shown to produce chaotic behaviour in the form of strange attractors. This chaotic behaviour is thought to lead to the collapse of the immune system.

It is also shown that the modelling of single viruses and the proliferation of frequency dependent CTL’s produces stable cycles. The paper concludes that the frequency dependence caused by the random search, with viral diversity (more than one virus), can make the behaviour of the system complex (for example quasi-periodic or chaotic). ‘*The frequency dependence leads to continuous alternating changes of the dominant, infected cells and corresponding specific immune cells so that chaotic behaviour will occur*’. The paper also shows that ‘*the interior equilibrium of the one-virus model can become unstable because of the frequency dependence’* and that the ‘*numerical simulation results suggest that only a stable limit cycle exists when the interior equilibrium is unstable’*. Finally concluding that the *‘numerical simulation results suggest that viral diversity can cause the emergence of chaotic behaviour’.*

[7] CTL’s (Cytotoxic T-lymphocytes) – Also known as T-Cells.

8. Ye, H., & Ding, Y. (2009). Nonlinear dynamics and chaos in a fractional-order HIV model. *Mathematical Problems in Engineering*, *2009*, 1–12. http://doi.org/10.1155/2009/378614 (H5 index 33, citations numbers:29)

Based on the research done by Iwami et.al in 2006, this article is taking into consideration the fractional order in HIV modelling. Their reasoning for considering their approach, is due to the fact that modelling with fractal differential equations proved beneficial for other systems such as the conductance of the biological membranes, as well as the fact that *'fractional order models possess memory while the main features of immune response involve memory*.'(Iwami, Nakaoka, & Takeuchi, 2006) Their goal is to observe the effect of such introduction to the dynamics of the system. The unstable internal equilibrium, present in the Iwami et al, is becoming asymptotically stable in this approach. When taking into consideration the viral diversity, strange chaotic attractors are present, thus *'chaos does exist in the fractional order HIV model with viral diversity'* (Ye & Ding, 2009).

The cases that used chaos theory for forecasting

The last category provides a series of cases where modelling with consideration of nonlinear dynamics enabled the authors to show greater accuracy in the short-term forecasting of populations.

8. Does Chaos Exist in Ecology? Evidence from a Rodent Population. Li B, Wang Y, Rong X, Su J, Wang R. International Journal of Nonlinear Sciences and Numerical Simulation, vol. 11, issue 6 (2010) (Cited by 2, International Journal of Nonlinear Sciences and Numerical Simulation H5 index: 10)

This paper is all about the dynamics of a rodent population (T. Triton, A long haired Hamster). In it, the authors show how, by applying different mathematical analyses, it is possible to reveal dynamics of populations that are closer to nonlinear, even chaotic patterns. The introduction to this paper talks directly about how the use of linear forecasting is inaccurate and somewhat limited in its reflection of actual population dynamics and the how the subsequent study is an attempt at improving this shortfall in accuracy.

In the analysis section of their report they point to the identification of nonlinearity in the population dynamics (p.470), this is, they say '*the necessary precondition for the detection of chaos, but not a sufficient precondition*'. Thus, there is an implication for the presence of chaos which can now be examined using Lyapunov exponent and correlation dimension analysis. The time series was later found to be chaotic, having a positive Lyapunov exponent, a usual indicator of chaotic behaviour. The analysis and prediction was done using a small data set algorithm to create short term predictions. Long term predictions were not easy to obtain owing to the complexities of wild data research. The authors also state that the intrinsic factors such as litter size, sex ratio and age structure were much more important and affecting than the extrinsic factors (climate, agricultural policies, and geographic condition) in determining population fluctuations.

Finally, the authors state that the goal of the paper was not to verify chaos but simply to acknowledge it as an important step in the forecasting of animal populations. It appears from the modelling that short-term prediction is possible, even fairly accurate but anything long term provides greater margins of error.

9. Equation-free mechanistic ecosystem forecasting using empirical dynamic modelling. Ye H, Beamish R, Glaser S, Grant S, Hsieh C, Richards L, Schnute J, Sugihara G. Proceedings of the National Academy of Sciences, vol. 112, issue 13 (2015) (Cited by 25, Proceedings of the National Academy of Sciences. H5 index: 215).

This paper shows a more modern perspective on modelling in ecology using no parameterizing equations. Parameterizing equations usually have fixed constants to represent environmental factors (growth rate, carrying capacity), but these can vary in time and relation to each other. By showing the application of these dynamical variables the paper claims a higher level of accuracy in the prediction of populations of sockeye salmon.

The paper begins by describing the evidence of nonlinear dynamics in the case of the guppy fish, whose preference for prey will vary depending upon its abundance or scarcity. Factors such as these are usually modelled as constants, unrelated to each other and are evidence of the nonlinearity in the dynamics of natural systems. The separation of these factors, it is supposed, leads to less accurate modelling when they are in fact deterministic and can be modelled as such. The authors go on to talk of the effect of causal variables and how it is difficult to determine which are the most important to identify due to negative and positive correlations. Incorrect selection of these variables leads to less accurate modelling. In the case of the Seymour-spawner recruit data[8], it was demonstrated that a correlation between surface sea temperatures and recruitment was unrealistically high, indicating an inaccurate relation between the selection variables of SST and consequent recruitment rate derived from analysis of it. The subsequent coupling of these variables as constants proved to provide less accurate data. Indicating that careful selection of variables provides important correlation information.

The authors then go on to demonstrate the presence of nonlinear dynamics using data from the previous 60 years and test the EDM[9] against another modelling technique (The Ricker technique)[10]. They go on to say '*In both cases, if the inclusion of environmental variables significantly improves forecast'.* Thus, demonstrating that the inclusion of dynamical variables (rather than static ones) improves results.

The paper concludes with a discussion of the data analysis and the confirmation of the hypotheses that the inclusion of nonlinear dynamics in population modelling yields more accurate results. EDM itself appears to provide an interesting method for highlighting the significance of environmental variables in dynamical modelling (particularly parameterizing) and aids by way of highlighting causal relationships between variables. Moreover, it can serve as a substitute for parametric equivalents.

The system: EDM (Empirical dynamical modelling) claims to '*recover the mechanistic relationship between the environment and population biology that fisheries models dismiss as insignificant'.* By applying Taken's embedding theorem, the system '*instead relies on time series data to reveal the dynamic relationships among variables as they occur'.*

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[8] *A comparative data set (Seymour is the name of the stock). Spawner recruit data is the number of spawning adult salmon.*
[9] *Empricial Dynamic Modelling. Explained more rigorously in the theory section. For a video of EDM please go here;* http://movie-usa.glencoesoftware.com/video/10.1073/pnas.1417063112/video-1

[10] *The Ricker technique gives the expected number of individuals in a generation as a function of the previous generation.*

10. Glaser, S. M., Fogarty, M. J., Liu, H., Altman, I., Hsieh, C. H., Kaufman, L., … Sugihara, G. (2014). Complex dynamics may limit prediction in marine fisheries. *Fish and Fisheries, 15*(4), 616–633. http://doi.org/10.1111/faf.12037
(Cited by 24, H5 index:45)

This article is using nonlinear models, of two different ecosystems, one consisting of fished species, and the other of unfished species, to '*quantify the predictability achievable'.* By comparing more than 200-time series, they can show that the dynamical behaviour of fished species is *'significantly different from the dynamics of the underlying fish population',* as the '*fished species are more likely to display nonlinear dynamics than unfished species'* (Glaser et al., 2014). This difference in dynamics was attributed to human intervention through fishing, and the nonlinearity caused an incline in the species to '*rapid and unpredictable population fluctuations that can severely impact food security and economic well-being (Mullon et al.2005) and highlighting the short time horizon over which these populations may be predictable'*(Glaser et al., 2014). When regarding the prediction, the authors found that 2-5 years' predictions are also limited, not only long term ones (>10 years). *'Over 1-year horizons, nonlinear models produced better forecasts for species with nonlinear dynamics than linear models did for species with linear-stochastic dynamics.* ' (Glaser et al., 2014) Their forecast was accurate in 70% of the time series, while for the remaining 30% of the time series, it is suggested that is due to the strong noise associated with the data. The article concludes with the fact that predictions of complex systems *'may be more limited than we would prefer.'* (Glaser et al., 2014)

5. Discussion

This project sought to investigate whether the development of a new theory-the theory of chaos -had any significant impact on population biology. Chaos theory revealed a new niche in the mathematical world that could not be seen before, mostly due to the linearization process. By not linearizing the data of dynamical systems, researchers could develop another way of modelling dynamical systems that led to several advantages, as well as some disadvantages.

In 1974, Robert May, whilst working with population models, discovered a rich dynamical behaviour that was overlooked due to the standard convention of linearization (May, 1974). This was the starting point of this project, as any influence of chaos theory in population biology emerged after this point. This seminal article, acknowledging the presence of chaos in biological systems, did not have a great impact initially, as over a decade later in 1989, Robert Pool states that; the majority of population biologists did not take into consideration chaos and that the data is only 'suggestive' of chaos (Pool, 1989). Several reasons for not considering chaos were found, among which were the noise levels of the data for population, which made it hard for the researchers to distinguish recognisable patterns, and that the data sets were usually not long enough to display chaotic behaviour (Pool, 1989).

Bearing these impediments in mind, in 1990 Robert May and George Sugihara published an article in Nature in which a method of distinguishing between chaos and noise (using Taken's embedding theorem) was created based on short term predictions (Sugihara & May, 1990). Chaotic time series predictions seem to be dependent on the prediction time interval, as the accuracy drops with increasing time, whereas unrelated noise predictions are independent of the period time interval (Sugihara & May, 1990). Robert May also went on to highlight 't*he pedagogical importance of studying nonlinear systems to counter balance the often-misleading intuition fostered by linearity and traditional education....'* (Sugihara & May, 1990).

For this project to be able to find an influence on population biology, chaos had to be recognized as being present in biological systems and accordingly considered when modelling them. Several research studies were conducted in which chaos was demonstrated to be present. For example, as early as 1979 a model of a predator prey interaction was found to have chaotic behaviour, in the form of a chaotic trajectory in the model (Gilpin, 1979). Even though his model is revealing chaos, the author is raising the problem of relevance: the degree that the model is resembling the real ecosystem (Gilpin, 1979). Models in general are just an imitation of complex dynamics, so in this case, the author is highlighting the problem of models in general: whether the model of predator prey is representative of the true nature of the ecosystem and can be improved somehow.

In 1984, a link between chaos and epidemics was found by Aron and Schwartz which demonstrated the presence of period doubling bifurcations in the model of epidemics (Aron & Schwartz, 1984). Evidence of chaos thus had begun to accumulate after only 10 years. The search for chaos in natural systems didn't stop, in 1991 researchers found a range of dynamical behaviour, including chaotic, in host-parasite interactions in insects (Hassell et al., 1991).

An important breakthrough came, due to the growing understanding of chaos as a part of biological systems, namely populations. In 2004, Petrovskii et. al could demonstrate a connection between chaotic behaviour and the paradox of enrichment (Petrovskii, Li, & Malchow, 2004). This explanation could become known mostly due to the acknowledgement of chaos theory and the significance of nonlinear dynamics, as the demonstration relies on including chaos, and considering it when modelling as a realistic consequence instead of simply linearizing.

Another point of reference when considering the influence of chaos on population biology was the presence of chaotic behaviour in HIV studies. As May hypothesized in 1989, chaos proved to be helpful in studying the interaction between the virus and the immune system (Pool, 1989). In 2006, Iwami et al. while studying the effect of viral diversity on the human immune system, found that the model was not stable without viral diversity, but also that the viral diversity can generate strange attractors (Iwami, Nakaoka, & Takeuchi, 2006). This article was not alone as just 3 years later, another article, that was considering fractals too, found chaos to be present in HIV models with viral diversity (Ye & Ding, 2009). We consider this evolution in the studies of models of HIV an important influence that the theory of chaos had upon population biology. Even though Ye and Ding are mentioning that the biological meaning of their model is to be further studied, progress has been made into understanding how the viral diversity influences the immune system, and it would have not been possible without reconsidering the ‘norm’, or standard linearization, in modelling dynamical systems.

Another important point in considering the influence of chaos theory on population biology are the consequences that it has on predictability. As implied by the name, in a state of chaos, no predictions can be made. We considered this point, and regarded several articles to understand what implications did this fact have on population biology.

To start with, a research paper from 2004 on rodent populations with data from 1982-2003, showed that the population was following a nonlinear, non-periodic and even chaotic dynamic (Li, Wang, Rong, Su, & Wang, 2010). They authors were also able to successfully do short term predictions about the *T. Triton* population (Li et al., 2010). Since the population clearly did not follow a linear model, we consider this example as a successful model with more accurate predictions. This article is not the only one that we considered in order to evaluate the influence of the theory of chaos in predictability in population biology. Sugihara and May, in 1990, not only developed a technique to distinguish between chaos and noise, but also compared predictions from 3 different populations: measles, chickenpox, and marine plankton, and the two types of approaches: non-linear and linear (Sugihara & May, 1990). The results varied, as for measles and marine plankton the nonlinear predictions seemed to fit the data better than the linear approach (Sugihara & May, 1990). For chickenpox though the predictions seemed to be the same either for the nonlinear approach or linear; the underlying reasons for this being either biological, such as the reproductive rates, or simple measurement data error as reporting of cases for chickenpox was not compulsory, compared to the measles (Sugihara & May, 1990).

A more recent article also used chaos theory in an empirical dynamical model and it was found that the model could make more precise predictions for the population of sockeye salmon than that of the pacific Salmon Population Commission’s non-inclusive model. The new model proposed by them estimated the population as being between 4.5 and 9 million whereas the Salmon Population Commission’s model estimated a value between 6.9 and 20 million fish, with the final number being 8.8 million (Glaser et al., 2014) (“Chaos Theory in Ecology Predicts Future Populations | Quanta Magazine,” n.d.). Predictions based on nonlinear models seem to be a better fit for data that is exhibiting nonlinear behaviour, but it is important to note that these predictions are usually short term as any long-term predictions are impossible due to the system's sensitivity to the initial conditions.

In 2013, researchers worked with non-linear forecasting models for fished and unfished species, using over 200 times series of survey abundance and landings; the two types of species showed different behaviour, as the fished species tended to display non-linear behaviour and the non-fished species linear behaviour. By comparing these two different mathematical behaviours, Glaser et al. could conclude that predictions over the fished species tended to be less accurate; over the period of one year, the predictions fit 70% of the cases while over a 5-year period the accuracy of the predictions declined exponentially (Glaser et al., 2014).

For this project, the articles provided us with the evidence that the inclusion and consideration of chaos instead of linearizing models of populations, has two effects: first, the short-term predictions are better and secondly, the long-term predictions are not accurate due to the core of chaos: sensitivity to the initial conditions. Our conclusions are based on the findings of the papers we have presented, although somewhat limited in their scope, there is a definite correlation in the findings. This could be somewhat attributed to our bias, after all we did select the papers ourselves deliberately, but we also looked at a lot of other papers and a theme was apparent. Initially cited by Robert May, it was regularly occurring throughout our research and proved to be unavoidable. Whilst we have only scratched the surface, one thing can be said for sure; Chaos theory has a place in population modelling.

Bibliometric data

Another consideration in the selection of our cases was that of the bibliometric data, although somewhat retrospectively, we did discover that some of the very many cited papers, mostly those of Robert May's showed a great interest in the work that was being done. Although over 30 years ago, 2 of these papers have been cited over 1000 times, a clear indication of the significance of them. The 1991 paper on population dynamics of insects shows a citation of 884, again a very large figure and an indication of sheer significance. This could be attributed to the fact that it was Robert May who wrote it, but for such a high number there must be something of importance going on here. Finally, the most modern papers on the fish species (sockeye salmon and marine) show citations of 24 and 25 respectively, although it only being 1 and 2 years since publication, this is another hint that the papers contain data that has value to others and significance in the scientific field.

6. Conclusion

The purpose of this report was to find what (if) any significant changes appeared in population biology after the theory of chaos was applied within the field. We found that significant changes appeared in two areas: modelling with nonlinear systems and predictability. Considering chaos in the modelling of dynamical systems gave rise to a new method of handling these systems: the rejection of linearization, and modelling them as nonlinear systems. This lead to several benefits, which were inaccessible before, as certain characteristics could not be seen in a linearized system. The second change that arose was in the field of predictability. The scientific world had to consider now, that there were well defined limits to predictability for nonlinear systems, long term predictions of which are virtually unfeasible. On the other hand, short term predictions for these systems appear to be becoming more accurate as the models are a better representation of the natural state and progression of the system. This short-term predictability (or lack of) has been observed for years in the form of weather predictions, the field in which Lorenz was working when he discovered chaos lurking in the models. Weather predictions tend to be useless after less than a week, and the underlying reason for this is, the sensitivity to the initial condition, the essence of chaos theory.

In conclusion, we found that chaos theory did have an influence on population biology, by helping to increase the understanding of natural systems and providing a new tool for modelling, as well as redefining the predictability of nonlinear systems and the consideration of nonlinear dynamics in population modelling.

7. Future perspectives

Given the limitations of time for this project, there was inevitably a great deal of information that was be left out, undiscovered or overlooked. There would also be a lot of detail yet to be uncovered and a greater depth at which we could delve into chaos theory. With this in mind, we considered a further six months or so on the project and what it would look like.

Although we uncovered, what we consider, the most significant characteristics of chaos theory, it is believed that there is a lot more to be understood. For example, the 15-year gap from Robert May's seminal paper on nonlinear forecasting is barely examined, this could prove to be an area rich in information. There is also the details themselves, somewhat complex and only generally applied and basically understood; it would be interesting to study the mathematics of chaos theory in a much greater depth, applying the knowledge with MATLAB scripts and real world data. A more thorough understanding is sure to be gained in this manner. Finally, the advent of EDM appears to be a new and exciting technique for dynamical modelling, one that it would have been fascinating to really explore in detail.

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