MATHEMATICAL ANALYSIS OF POPULATION GROWTH SUBJECT TO ENVIRONMENTAL CHANGE

A thesis submitted for the degree of
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Many ecosystems are pressured when the environment is perturbed, such as when resources are scarce, or even when they are over-abundant. Changes in the environment impact on its ability to support a population of a given species. However, most current models do not take the changing environment into consideration. The standard approach in modelling a population in its environment is to assume that the carrying capacity, which is a proxy for the state of the environment, is unchanging. In effect, the assumption also posits that the population is negligible compared to the environment and cannot alter the carrying capacity in any way. Thus, modelling the interplay of the population with its environments is important to describe varying factors that exist in the system. This objective can be achieved by treating the carrying capacity as time- and space-dependent variables in the governing equations of the model. Thereby, any changes to the environment can be naturally reflected in the survival, movement and competition of the species within the ecosystem. In this thesis, detailed investigations of several mathematical models for population growth are presented. Formulating the carrying capacity as being time-dependent was the fundamental approach used to describe a varying environment which resulted in investigating a non-autonomous equation. This approach led to developing models that directly couple the dynamics of one or two species with their environments. To attain this, the carrying capacity was modelled as a state-variable. In these models, the ultimate state for the ecosystem depends on the resource enrichment parameter that was found to have significant impact on the growth of a population, leading to either coexistence or extinction of a particular species. Other dynamical behaviours including oscillations in population have also been found to exist. Varying the carrying capacity has given a better understanding of population growth when subjected to environmental change. This thesis serves as another platform for ecologists and biologists to investigate further the importance of a varying environment, and could be applied in future population-growth studies.

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Abstract

Many ecosystems are pressured when the environment is perturbed, such as when resources are scarce, or even when they are over-abundant. Changes in the environment impact on its ability to support a population of a given species. However, most current models do not take the changing environment into consideration. The standard approach in modelling a population in its environment is to assume that the carrying capacity, which is a proxy for the state of the environment, is unchanging. In effect, the assumption also posits that the population is negligible compared to the environment and cannot alter the carrying capacity in any way. Thus, modelling the interplay of the population with its environments is important to describe varying factors that exist in the system. This objective can be achieved by treating the carrying capacity as time- and space-dependent variables in the governing equations of the model. Thereby, any changes to the environment can be naturally reflected in the survival, movement and competition of the species within the ecosystem.

In this thesis, detailed investigations of several mathematical models for population growth are presented. Formulating the carrying capacity as being time-dependent was the fundamental approach used to describe a varying environment which resulted in investigating a non-autonomous equation. This approach led to developing models that directly couple the dynamics of one or two species with their environments. To attain this, the carrying capacity was modelled as a state-variable. In these models, the ultimate state for the ecosystem depends on the resource enrichment parameter that was found to have significant impact on the growth of a population, leading to either coexistence or extinction of a particular species. Other dynamical behaviours including oscillations in population have also been found to exist.

Varying the carrying capacity has given a better understanding of population growth when subjected to environmental change. This thesis serves as another platform for ecologists and biologists to investigate further the importance of a varying environment, and could be applied in future population-growth studies.

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Published work

The following publications correspond to work within this thesis:

1. **H. Safuan**, I. N. Towers, Z. Jovanoski and H. S. Sidhu, *A simple model for the total microbial biomass under occlusion of healthy human skin,* In Chan, F., Marinova, D. and Anderssen, R.S. (eds) MODSIM 2011, 19th International Congress on Modelling and Simulation. Modelling and Simulation Society of Australia and New Zealand, December 2011, pp. 733–739.
`http://www.mssanz.org.au/modsim2011/AA/safuan.pdf`
(based on part of the work in Chapter 3)
2. **H. M. Safuan**, I. N. Towers, Z. Jovanoski and H. S. Sidhu, *Coupled logistic carrying capacity model,* ANZIAM J.(E), **53**, pp. C142–C154, 2012.
`http://journal.austms.org.au/ojs/index.php/ANZIAM/article/view/4972`
(based on part of the work in Chapter 4)
3. **H. M. Safuan**, Z. Jovanoski, H. S. Sidhu and I. N. Towers, *Exact solution of a non-autonomous logistic population model,* Ecological Modelling, **251**, pp. 99–102, 2013. `http://dx.doi.org/10.1016/j.ecolmodel.2012.12.016`
(based on part of the work in Chapter 3)
4. **H. M. Safuan**, H. S. Sidhu, Z. Jovanoski and I. N. Towers, *Impacts of biotic resource enrichment on a predator-prey population,* Bulletin of Mathematical Biology, **75**, pp. 1798–1812, 2013.
`http://link.springer.com/article/10.1007/s11538-013-9869-7`
(based on part of the work in Chapter 5)
5. **H. M. Safuan**, H. S. Sidhu, Z. Jovanoski and I. N. Towers, *A two-species predator-prey model in an environment enriched by a biotic resource,* ANZIAM J.(E), **54**, pp. C768–C787, 2014. `http://journal.austms.org.au/ojs/index.php/ANZIAMJ/article/view/6376`
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6. **H. M. Safuan**, I. N. Towers, Z. Jovanoski and H. S. Sidhu, *On travelling wave solutions of the diffusive Leslie-Gower model,* Manuscript submitted for publication, 2014.
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7. **H. M. Safuan**, H. S. Sidhu, Z. Jovanoski and I. N. Towers, *On travelling wave solutions of predator-prey model with resource enrichment,* Manuscript in preparation, 2014.
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The following oral presentations were given based on work presented in this thesis:

1. UNSW Research Day 2011, *A model for total cutaneous microbial biomass during occlusion of healthy human skin*, October 2011, UNSW Canberra, Australia. (based on part of the work in Chapter 3)
2. 2011 ACT-NSW ANZIAM Joint Mini-meeting, *Coupled logistic carrying capacity model*, November 2011, Murramarang, New South Wales, Australia. (based on part of the work in Chapter 4)
3. The 10th Engineering Mathematics and Applications Conference (EMAC 2011), *Coupled logistic carrying capacity model*, December 2011, Sydney, Australia. (based on part of the work in Chapter 4)
4. The 19th International Congress on Modelling and Simulation (MODSIM 2011), *A simple model for the total microbial biomass under occlusion of healthy human skin*, December 2011, Perth, Australia. (based on part of the work in Chapter 3)
5. The 16th Biennial Computational Techniques and Applications Conference (CTAC 2012), *A two species population growth model with varying carrying capacity*, September 2012, Queensland, Australia. (based on part of the work in Chapter 5)
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Posters were also presented based on work in this thesis:

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   (based on part of the work in Chapter 3)
2. UNSW Research Day 2011, *A model for total cutaneous microbial biomass during occlusion of healthy human skin*, October 2011, UNSW Canberra, Australia.
   (based on part of the work in Chapter 3)
3. UNSW Research Day 2012, *A predator-prey population model with varying carrying capacity*, October 2012, UNSW Canberra, Australia.
   (based on part of the work in Chapter 5)

The following awards were received during my candidature:

1. 3rd place of Poster Competition “Judges Selection” (UNSW Research Day 2011), October 2011.
2. Best student talk at the Joint ACT-NSW ANZIAM Meeting 2011, November 2011.
3. Funding from the CSIRO/ANZIAM student support scheme to attend the 10th Engineering Mathematics and Applications Conference (EMAC 2011), Sydney, December 2011.
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CHAPTER 1

Introduction

In this thesis, we investigate several mathematical models of population growth subjected to changing environments. We start with a fundamental model which is then extended to both spatially independent and dependent models. The main aims of this thesis are to:

1. investigate changing environments by treating carrying capacities as variables in both time and space;
2. develop mathematical models to describe the interactions between one or more species sharing the same biotic resource through each individual species' carrying capacity;
3. investigate the impacts of biotic resource enrichment on a population;
4. broaden the model to a spatial system to observe the dynamics of local dispersal and competition that will affect population distribution.

1.1 Background

The feedback between a population and its environment is the underlying concept in the study of population ecology, as population growth and decay are greatly affected by changes in the environment. The diversity of elements such as nutrients, food sources, weather and types of biological species are important factors in the degradation of (or improvement in) surrounding habitat and also in maintaining the sustainability of species for which the environment is unlikely to remain constant.

Besides changes in temperature and/or moisture that could correspond to changes in the environment, other biophysical factors, such as the introduction of a new species in a habitat, for instance a consumer (predator) or resource (prey), can be measured as an environmental change. Sometimes, this can ultimately modify the composition, biomass and distribution of a species in an ecosystem. For example, the bio-manipulation of an ecosystem or food-web system through modifications in nutrients, zooplankton and fish populations is vital for the maintenance and enhancement of water quality in a lake or sea. A predator species was introduced into Round Lake, Minnesota to observe its effect on the phytoplankton and zooplankton communities, as well as on the total nutrient concentrations [Shapiro and Wright, 1984]. This experiment altered the compositions of marine species in that lake after two years. It was observed that phytoplankton and zooplankton numbers decreased and, notably, a rare situation in which a herbivore species (*Daphnia*) became the dominant genus. This proved that changes in the primary environment of an ecosystem have a great effect and can restructure the compositions of species. Related work can be found in Chess et al. [1993] and Wahl et al. [2011].

In another example, a population living in a confined habitat, such as an island, will collapse if the environment's fundamental resources are over-exploited, for example, the reindeer populations on St. Paul Island, Alaska [Scheffer, 1951, Huzimura and Matsuyama, 1999] and St. Matthew Island, Alaska [Klein, 1968]. Their "boom-and-bust"population explosions illustrated how over-abundances of that species exhausted the available resources in an environment not conducive to supporting it, and eventually drove the species to extinction. A similar scenario is thought to have occurred in the human population on Easter Island, Chile [Basener et al., 2008, Bologna and Flores, 2008, Sprott, 2011], where environmental degradation was caused by over-exploitation of the island's fundamental resources.

However, even an enriched resource can turn out to be a detrimental environment for populations. Studies of intraguild predation (a mixture of competition and predation) have found the possibility of a population being extinguished due to an environmental change (resource enrichment) [Polis et al., 1989, Polis and Holt, 1992, Holt and Polis, 1997, Mylius et al., 2001]. Increasing resources only benefits the top predator, usually an omnivore, while suppressing other populations (prey/consumer) from the food chain. All these examples are evidence that a change in the environment can significantly affect the food-chain system.

As maintaining existing resources and the environment are crucial for the survival of populations, environmental control, management and modelling have become significant. One approach is developing realistic mathematical models to predict populations' behaviours when subjected to varying environments. Although it has been a challenge for mathematicians, biologists and ecologists to formulate a model that could describe all possible factors, in the long run ecologists and biologists have benefitted from mathematical models designed and developed through careful analysis and various trial-and-error techniques that can describe the complex dynamics of a population and its environment. These models constantly serve as the main theoretical approach for studying populations' behaviours in a wide range of possible scenarios.

As varying environments provide a more meaningful subject for consideration than those that are constant, it is the aim in this thesis to explore and analyse population models subjected to changing environments.

1.2 Carrying capacity

Generally, the carrying capacity defines the maximal abundance of a population an environment can sustain given finite resources, and is also considered the limiting factor for an ecosystem or population. Its concept is extensively applied in many areas such as population dynamics, biology, ecology, economics, technology, agriculture and even cultural and social studies. There are several schools of thought regarding this concept which have debated its application in population ecology and other areas [Dewar, 1984, Scarnecchia, 1990, Price, 1999, Seidl and Tisdell, 1999, del Monte-Luna et al., 2004].

Dewar [1984] explained two concepts of the carrying capacity as it being a feature of the environment or changes in a population's growth rate and density. Although he suggested that both are unlikely to be uniformly directly related, most studies in applied ecology and mathematical ecology have regarded them as strongly linked. In fact, in some studies, the carrying capacity has been observed to be a mixture of both [Coleman, 1979a, Samanta and Maiti, 2004, W. Hsin-i and Kenerley, 2009]. Dewar [1984] agreed that no environment is unchanging, and therefore the carrying capacity should vary. McLeod [1997] argued that the concept of the carrying capacity is useful in variable environments and found that it could be adapted in a deterministic model or slightly variable environment, but not in a stochastic one.

Without carrying capacities (in other words, if population growth is not controlled), our world and its entire ecosystem would collapse due to the scarcity of resources, environmental pressures and health issues. For example, the offspring of a female housefly would cover the whole Earth's surface in a short time if its population growth were not controlled, as it is able to reproduce over 5 trillion houseflies in a year. Also, under certain circumstances, a bacterium would form a layer a foot deep over the entire Earth's surface in less than 2 days due to its capability to reproduce itself every 20 minutes [Miller, 2007]. These are examples of rapid exponential growth whereby populations grow indefinitely and "explode". However as in reality, populations are finite and limited, there must be some bounds within which they increase, crowd and stabilise; their growth could be restricted by the amounts of available resources such as food, water, space and the environment.

Attempts have been made to estimate the Earth's carrying capacity [Cohen, 1995, Hopfenberg, 2003, Berck et al., 2012] but, as the human population is dynamic, it is rather difficult to estimate its exact carrying capacity. As humanity is capable of modifying the environment and improving the production of resources, using continually developing technologies, there are definitely interactions between humans and the Earth's human carrying capacity. The human population model proposed by Cohen [1995] depends strongly on the ability of humans to increase or decrease the carrying capacity. Therefore, it uses a variable carrying capacity whereby each additional person impacts on the carrying capacity by an amount that depends on the resources available, and his/her capability to contribute to any positive/negative production for the human population. To date, Cohen's model remains a possible projection of human populations over the next hundred years.

To estimate the carrying capacity of non-human species, it is necessary to make some assumptions, as there are many factors that contribute to the development or destruction of the environment's carrying capacity. Factors that affect the population environment are classified as biotic or abiotic resources [Price, 1999, del Monte-Luna et al., 2004]. An abiotic resource is non-living, for example water, nutrients, temperature and even toxicants that enter the population's environment. On the other hand, a biotic resource is one that grows, reproduces and is usually self-limiting, for example an additional living species that serves as a resource for an original population. In terms of these two factors, a constant carrying capacity may not be applicable for describing populations' changing environments and to provide a realistic scenario, so that a variable carrying capacity should be considered when modelling them.

A review by del Monte-Luna et al. [2004] detailed the versatile concepts of the carrying capacity for populations, communities, ecosystems and the biosphere, and proposed a definition compatible with various applications as

> *"the limit of growth or development of each and all hierarchical levels of biological integration, beginning with the population, and shaped by processes and independent relationships between finite resources and the consumers of those resources"* [del Monte-Luna et al., 2004].

From this review, the carrying capacity can be summarized as the maximal capacity of the environment to sustain a given species within the restrictions of certain biological resources (biotic and/or abiotic).

Mathematically, the carrying capacity is a fixed parameter or a variable K in the classic logistic model discussed in the next section. In modern ecology, an ever-changing resource in an environment is an intriguing aspect to study. In this thesis, mathematical models to describe the changes in an environment through a variable carrying capacity are investigated and developed.

1.3 Population-growth model and carrying capacity

Population-growth modelling is a research area in the fields of mathematical biology and ecology due to its importance in various ecosystems. With the rich dynamics populations are capable of displaying, they make for interesting investigations. The logistic equation is an example of growth models that has been widely studied and applied in population and ecological modelling. Introduced in the 19th century, it describes population growth using a self-limitation term which serves as a correction to the unlimited growth of the Malthusian model, commonly referred to as the exponential model. The classic logistic (or Verhulst's) equation is [Murray, 1989, Banks, 1994]

$$\frac{dN(t)}{dt} = rN(t)\left[1 - \frac{N(t)}{K}\right], \qquad N(0) = N_0. \tag{1.1}$$

Equation (1.1) is autonomous as the parameters r and K are constant. Its nature is such that the properties of the solutions, for all strictly positive initial conditions, approach the constant value of the carrying capacity, K, as time, t, tends to infinity (Figure 1.1). If the population starts at a level well below the carrying capacity, K, the population first increases steadily, then rapidly, due to the linear term, until it approaches an inflection point (at which the growth rate is maximal). After passing the critical point, the population's reproduction rate declines due to the crowding effect of individuals competing for limited resources; after experiencing this environmental pressure, the population stabilises. If the population starts at a higher value than the carrying capacity K, then population growth rate is negative, with its number decreasing and reaching a plateau. The solution to Equation (1.1) is obtained by separation of variables as

$$N(t) = \frac{KN_0}{Ke^{-rt} + N_0(1 - e^{-rt})}. \tag{1.2}$$

Another growth model widely used for modelling population growth is the Gompertz model, which is similar to the logistic equation (1.1) in terms of its sigmoid shape, clear inflection point and being analytically solvable [Banks, 1994].

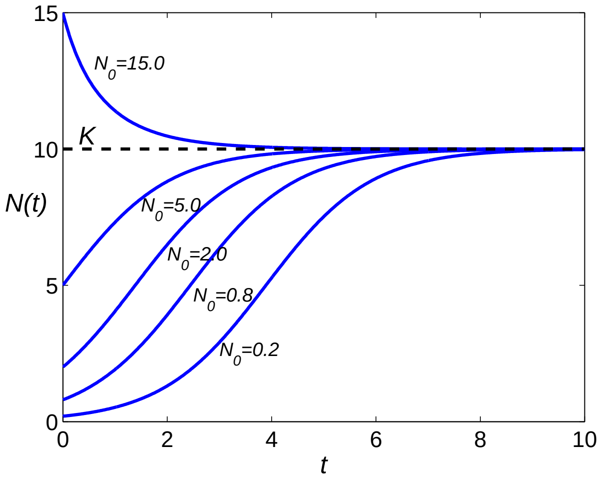


Figure 1.1: Logistic growth curves with constant K for various initial conditions, N_0. The carrying capacity is $K = 10$.

The Gompertz model is written as

$$\frac{dN(t)}{dt} = rN(t) \ln \left(\frac{K}{N(t)} \right) \tag{1.3}$$

The Gompertz model is commonly applied in cancer research [Xu, 1987, Domingues, 2012, Gerlee, 2013]. The difference between the logistic and the Gompertz model is how fast the population, $N(t)$, approaches its limiting value, as reflected by the "skewness" of the curvature [Winsor, 1932]. The Gompertz curve increases slowly initially, and gradually increases asymmetrically when approaching its asymptote, whereas the logistic curve reaches its asymptote symmetrically about the inflection point. The inflection points of the Gompertz and logistic models occur at K/e and $K/2$, respectively. Figure 1.2 shows a comparison of the growth curves of the exponential, logistic and Gompertz models.

As the Gompertz and logistic models possess similar shapes and properties, it is best to first investigate the simpler model and analyse its dynamics. Thus, the logistic equation establishes the framework for the model in this thesis because it is simple and the most widely used for investigating population growth.

As discussed in the previous section, assuming that the carrying capacity is constant is not often realistic in many applications, especially in modelling populations. Thus, many studies have discussed an alternative approach by investigating the importance of time-dependent carrying capacities, $K = K(t)$, embedded in a non-autonomous logistic equation [Coleman, 1979a, Ikeda and Yokoi, 1980, Hallam and Clark, 1981, Banks, 1994, Meyer, 1994, Meyer and Ausubel, 1999, Shepherd

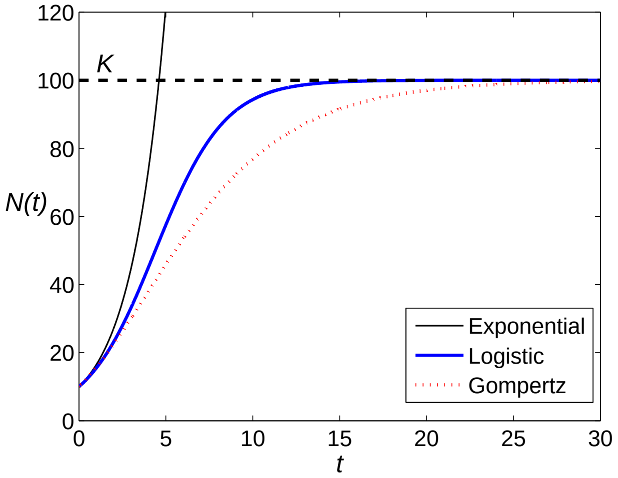


Figure 1.2: Exponential, logistic and Gompertz growth curves with $N_0 = 10$. The carrying capacity is $K = 100$.

and Stojkov, 2007, Trappey and Wu, 2008, Rogovchenko and Rogovchenko, 2009, Grozdanovski and Shepherd, 2007, Grozdanovski et al., 2009, 2010]

$$\frac{dN(t)}{dt} = rN(t)\left[1 - \frac{N(t)}{K(t)}\right], \qquad N(0) = N_0. \tag{1.4}$$

The general mathematical properties of Equation (1.4) were introduced by Coleman [1979a] to model a changing environment. Hallam and Clark [1981] studied the non-autonomous logistic equation in a deteriorating environment which always leads to extinction of the population. A series of works has been done since then, extending the idea of time-dependent carrying capacities to toxicants in the population and toxicants in the environment [Hallam and Clark, 1983, Hallam et al., 1983, Freedman and Shukla, 1991, Samanta and Maiti, 2004].

The effect of a nutrient enrichment in an inland sea on the fish population was studied by Ikeda and Yokoi [1980]. In their work, nutrient enrichment is described by an increase in the carrying capacity of plankton, which are the food source for small fish. In other applications, time-dependent carrying capacities have been used to represent seasonal environments [Coleman et al., 1979b, Leach and Andriopoulos, 2004, Rogovchenko and Rogovchenko, 2009]. Seasonal environments, such as those with temperature variations, can affect population reproduction rates especially in bacteria. Further, oceanic tides are responsible for fluctuations in the numbers of various aquatic organisms and their ecosystems, while rainfall influences the food availability for a population.

In modelling the human population in the modern world, its carrying capacity has been associated with the development of technological innovations. Studies by Meyer [1994] and Meyer and Ausubel [1999] employed a variable carrying capacity in the application of technological developments to a human population. Later, Watanabe et al. [2004] used a sigmoidal function to model the carrying capacity to compare trends in various technological goods. In another application, a similar form of the sigmoidal carrying capacity was used to model the body size of a host infected by parasites [Ebert and Weisser, 1997]. Hahnfeldt et al. [1999] and Sachs et al. [2001] introduced a carrying capacity proportional to the amount of neovascularisation in a Gompertz model of tumor growth.

A carrying capacity which depends on a natural habitat has also been studied as a changing environment. Experiments by Griffen and Drake [2008] demonstrated that improving a population's carrying capacity, as demonstrated by improving its habitat quality, increased its permanence. A logistic model was used by Huang et al. [2012] to represent the rate of habitat deterioration for freshwater cetacean species. For a relatively low habitat deterioration rate, fluctuations in the populations were found, whereas a sharp increase in the rate forced the population to decline and, in some cases, disappear from the system.

Gonzalez et al. [2008] modified the work of Gurney and Lawton [1996] to investigate a two-species population model consisting of a resident and an invader species. In the work of Gonzalez et al. [2008], both species competed for a habitat that was formulated as the carrying capacity of each species, and for which the habitat itself varied over time. They found that the invader species could change, adapt to and dominate the local environment due to its ability to affect the flow of resources. If the activities of a population affect its own carrying capacity, such as by enhancing or polluting resources, its carrying capacity is dependent on the population, N, itself, $K = K(N)$, which could also involve a delay process in the system [Yukalov et al., 2012].

For these applications, it is vital that the carrying capacity is not treated as a constant. Positive changes in the environment, such as new resources or food production, increases the carrying capacity, whereas a negative change such as the advent of a toxic environment or food depletion, decreases the carrying capacity.

In this thesis, a functional form of the carrying capacity is proposed to represent the development of a population environment using a monotonically increasing function. Although Ikeda and Yokoi [1980] used this specific form to model the enrichment of nutrients in an inland sea, the carrying capacity in this thesis is incorporated in the logistic equation (1.4) and applied to bacterial populations. As, to the best of our knowledge, this work has never been undertaken before, we begin by investigating a simple yet useful model. Its parameters are derived from published experimental data, independently verified using another set of data.

As well as the carrying capacity taking various time-dependent forms, $K(t)$, the carrying capacity is formulated as a variable-dependent form. If the carrying capacity is dependent on another component, i.e. an abiotic or biotic resource which also changes with time, the system can be written in the form

$$\frac{dN}{dt} = rN\Big(1 - \frac{N}{K}\Big), \tag{1.5a}$$

$$\frac{dK}{dt} = f(N, K), \tag{1.5b}$$

where $f(N, K)$ is a function involving linear or non-linear interaction terms between population, N, and carrying capacity, K. In contrast to a non-autonomous equation with a time-dependent carrying capacity, a model with variable-dependent carrying capacity can be an autonomous system, and the coupled rate equations can be analysed using standard tools, such as linear stability and phase-plane analyses. Interesting dynamics can also be seen if more-complex interaction terms between the population and its carrying capacity are involved in system (1.5).

One of the simplest models has been studied by Huzimura and Matsuyama [1999] for a deer population with its primary resource (lichen). It assumed that the carrying capacity in the logistic growth of deer was resource-dependent and was depleted through the consumption of lichen by the deer. Another model that treats the carrying capacity as a state-variable was studied by Thornley and France [2005]; the carrying capacity in this case depended on the current values of environmental variables that could cause the final value of the carrying capacity to increase or decrease depending on parameter settings.

In this thesis, we focus on the concept of an environmental carrying capacity as a biotic resource. The population alters its carrying capacity by interacting with its environment. To model this, the reproductive and death terms of the biotic resource should be included, in addition to the growth equation of the population. Although the idea of a biotic resource has been included in Huzimura and Matsuyama [1999] as a linear term, the effect of the nonlinear terms are analysed here and the results presented. The results obtained in our work are compared to those found in their work and that of Thornley and France [2005].

There are studies that took into account the over-exploitation of the primary resources, such as trees on an isolated island, that led to the collapse of the society inhabiting that island. A study by Basener and Ross [2005] incorporated limited self-replenishing resources, such as trees and plants, in the carrying capacity of the human population living on Easter Island. By drastically harvesting this abundant resource, eventually its supply deteriorated and the population was driven to extinction. Degradation of the environment can also be exacerbated by the introduction of other inhabitants, such as a pest population, for example, rats [Basener et al., 2008, Sprott, 2011]. In another study, the model in Sprott [2011] is rewritten as

$$\frac{dX}{dt} = r_1 X\Big(1 - \frac{X}{K}\Big), \tag{1.6a}$$

$$\frac{dY}{dt} = r_2 Y\Big(1 - \frac{Y}{K}\Big), \tag{1.6b}$$

$$\frac{dK}{dt} = f(X, Y, K), \tag{1.6c}$$

where $f(X, Y, K)$ involves interactions among humans, X, rats, Y, and trees, K. In the work of Basener and Ross [2005], a periodic solution exists in a certain range of parameters that demonstrates persistent fluctuations between species. Sprott [2011] found that, in a narrow range of parameters, periodic solutions and chaos existed in the system, with chaos having the characteristic of random population fluctuations.

Another situation that is related to a resource-dependent carrying capacity is a predator-prey type model. Assuming that the carrying capacity of a predator's environment is proportional to the abundance of its prey, we can write a system of ratio-type predator-prey equations. This type of model introduced by Leslie [1958] and Leslie and Gower [1960], and work related to it has continue to the present day [Korobeinikov, 2001, Wang et al., 2003, Seo and Kot, 2008, Chen et al., 2009, Chen and Chen, 2009, Li and Li, 2013, Yang and Li, 2014]. Although, generally, the model consists of a predator and prey with nonlinear interaction terms, it is not restricted to only two species but can be extended to three or more in a food-chain model [Gakkhar and Naji, 2003, Korobeinikov and Lee, 2009].

Most studies involving predator-prey systems have presumed that the carrying capacity of a predator is dependent on only its prey, without considering the carrying capacity of the prey, which is also dependent on another species, that is the base resource. Even though there exist intraguild models (in which the predator and prey share the same resource), they do not incorporate variable carrying capacities [Mylius et al., 2001, Diehl and Feissel, 2000, 2001, Hin et al., 2011].

In this thesis, we develop models of two species with carrying capacities as functions of a shared biotic resource, using the concept of a ratio-dependent type of predator-prey models. The general model can be written as

$$\frac{dX}{dt} = r_1 X\Big(1 - \frac{X}{pK}\Big) - aF(X)Y, \tag{1.7a}$$

$$\frac{dY}{dt} = r_2 Y\Big(1 - \frac{Y}{qK}\Big) + bF(X)Y, \tag{1.7b}$$

$$\frac{dK}{dt} = f(X, Y, K). \tag{1.7c}$$

Stability and bifurcation analyses of model (1.7) are performed, focussing on an environmental change whereby the enrichment of the resource has a great effect on perturbing the system's behaviour from one stable steady-state to another in the system. Other dynamics found in this system are discussed and presented.

Non-spatial models, such as ordinary differential equations (ODEs), which depend on a single variable serve as primary and significant platforms for investigating dynamical systems. To include a spatial dimension, partial differential equations (PDEs) must be considered. Applying them to ecological modelling is well established, as reviewed by Holmes et al. [1994] while more detailed explanations of diffusive and non-diffusive population models were discussed by Jungel [2010]. The Fisher equation is a classic example of a PDE for a single-species population,

$$\frac{\partial u(\mathbf{r}, t)}{\partial t} = D\nabla^2 u(\mathbf{r}, t) + ru(\mathbf{r}, t)\left[1 - \frac{u(\mathbf{r}, t)}{K}\right], \tag{1.8}$$

where $\mathbf{r} = (x,\ y,\ z)^\intercal$, $u(\mathbf{r}, t)$ is the time-dependent population density, and D the diffusion coefficient. Equation (1.8) has a travelling wave solution with a specific wave speed. The equation was introduced to describe the spreading of a favoured gene in a population [Fisher, 1937]. The wavefront solution provides information on how populations disperse over space. For a system with a two-species population, Dunbar [1983] investigated a diffusive predator-prey model that gave rise to a travelling wave solution in which the travelling wave moved with a constant shape and speed.

In this thesis, a travelling wave solution for a predator-prey ratio-dependent type of model with diffusion is investigated. The wave speed and the effects of the diffusivity parameters for each species over a spatial domain are analysed. For a food-chain model that involves more than two species, the ODE model is extended to a PDE system, and the travelling wave solution that arises in the predator-prey model with a shared-resource model is investigated. Numerical solutions and simulations are presented to illustrate the system's dynamics.

1.4 Overview of thesis

The aim of this thesis is to develop and analyse population-growth models subject to changing environments, modelled through variable carrying capacities. It is organised as follows:

Chapter 2 introduces the mathematical methods and tools that are used to investigate and analyse the mathematical models in this thesis, and provides a brief introduction to bifurcation analyses, in particular cusp singularity and Hopf bifurcation. Software packages which are used to analyse the models are also presented in this chapter.

Chapter 3 introduces the fundamental, non-autonomous logistic model, and various functional forms of the carrying capacity, $K(t)$. A logistic model with a saturating carrying capacity is developed and applied to describe the total microbial biomass under an occlusion of healthy human skin. Data from published work are used to inform modelling decisions, and successfully verified and published in Safuan et al. [2011]. A derivation of the exact solution for the developed model is also discussed in this chapter, based on Safuan et al. [2013a].

Chapter 4 introduces modified logistic models which consider the carrying capacity as a state-variable. A logistic model limited by its carrying capacity to represent a simple biotic resource, based on Safuan et al. [2012], is also discussed.

Chapter 5 introduces two-species population-growth models with variable carrying capacities. The concepts of the ratio-dependent type model, as well as the food-chain model are applied to modified predator-prey systems, with the carrying capacity modelled to represent a third species — a biotic resource. The carrying capacity is taken to be proportional to a biotic resource, and both species can directly alter the density of the biotic resource by interacting with it. The proposed models can be linked to intraguild predation models in which the predator and prey share the same resource. Taking the enrichment parameter of the resource as the bifurcation parameter, Hopf bifurcations are found for some parameter ranges, which generate solutions that possess limit-cycle behaviour. An analysis of the Hopf bifurcation was given in Safuan et al. [2013b]. In a slightly different model, the bistability in certain parameter regions describes the transition from a beneficial to a detrimental environment [Safuan et al., 2014b]. Special cases of these systems are examined, and the possibility of permanence and (or) extinction of species presented.

Chapter 6 introduces a one-dimensional spatially dependent population-resource model. The existence of travelling wave solutions and the minimum wave speed relationship are investigated. A linear stability analysis is performed in addition to a full numerical simulation of the model. Using the method of lines, the PDE systems are numerically solved for several types of initial conditions, and the corresponding travelling wave solution is demonstrated, as discussed in [Safuan et al., 2014c] (Manuscript submitted for publication). A similar analysis is applied to the diffusive two-species population model with a shared biotic resource, whereby the travelling wave solution of the model is studied and its dynamics investigated [Safuan et al., 2014a] (Manuscript in preparation).

Chapter 7 concludes this thesis by summarising all the main results from the study and discussing possible extensions to the models presented.

Chapter 2

Mathematical methods and tools

In this chapter, the mathematical tools, programs and software packages that are used throughout this thesis to analyse the mathematical aspects of various population models are introduced. Some parts of this chapter are discussed in Safuan et al. [2014b].

2.1 Mathematical methods

In this section, the bifurcation and singularity analyses used in Chapter 5, and the travelling wave solution applied in Chapter 6 are briefly introduced.

2.1.1 Bifurcation analysis

Bifurcation is defined as “splitting into two”, and is used to describe a change that occurs in a system by varying certain parameters [Arnol’d, 1994]. There are many types of bifurcation that can exist in dynamical systems, such as saddle-node, transcritical and Hopf.

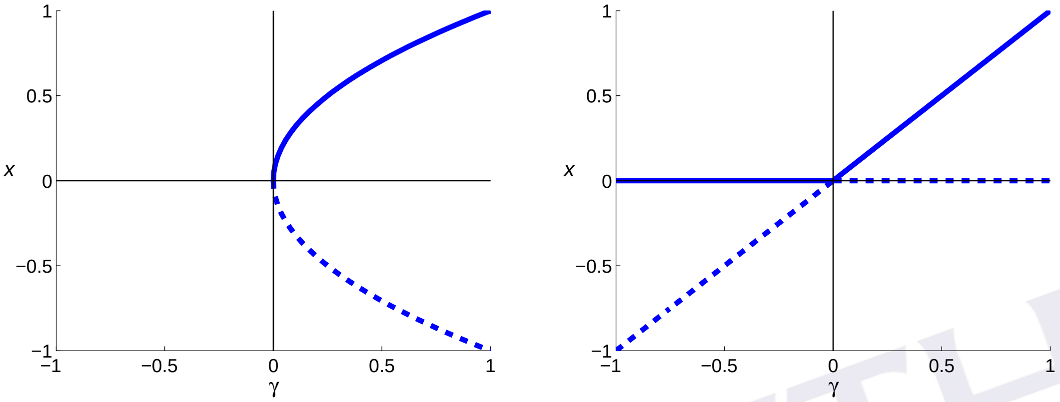
Consider a one-dimensional system in the form

$$\frac{dx}{dt} = f(x, \gamma),$$

where x is a state-variable and γ the parameter to be varied. This parameter, γ, is referred to as a bifurcation parameter. By varying the value of this bifurcation parameter, different types of dynamics emerging in the steady-state solution may be observed. Bifurcation diagrams play an important role in helping to graphically illustrate these dynamics.

Saddle-node bifurcation

A saddle-node bifurcation is a type of local bifurcation that occurs when a zero of a vector field has a linearisation with zero determinant (at least one of the eigenvalues is zero) [Hubbard and West, 1995]. The creation and destruction of a steady-state is another way of defining it. This type of bifurcation is often also referred to as *a turning point*, *limit point* or *fold bifurcation*. Figure 2.1a shows an example of a saddle-node bifurcation, with the point located at $\gamma = 0$ marking the turning point between the stable (solid line) and the unstable (dashed) steady-states.



(a)

(b)

Figure 2.1: Examples of bifurcation: (a) saddle-node bifurcation; and (b) transcritical bifurcation (solid line – stable steady-state, and dashed line – unstable steady-state).

Transcritical bifurcation

A transcritical bifurcation occurs when two steady-state branches collide at an intersection referred to as a bifurcation point (Figure 2.1b.). The stability along each branch changes after passing through $\gamma = 0$. In Figure 2.1b, one of the steady-states is stable if the bifurcation parameter, γ, is less than zero, but becomes unstable otherwise, while the opposite applies for the other steady-state branch.

2.1.2 Singularity analysis

Singularity theory [Golubitsky and Schaeffer, 1979, 1985a,b] is a convenient approach to determine regions which show different steady-state behaviours. Generally we start by reducing a physical system to a non-linear implicit scalar equation, sometimes called a singularity function, which helps to determine the behaviour of the steady-state solution. Consider a system of two differential equations in the form

$$\frac{dx}{dt} = f(x, y, \gamma, \mathbf{p}), \tag{2.1a}$$

$$\frac{dy}{dt} = g(x, y, \gamma, \mathbf{p}), \tag{2.1b}$$

where x and y are the state-variables of the system, γ the main primary bifurcation parameter, and $\mathbf{p}$ all other parameters, which are often called secondary bifurcation parameters. Setting both equations to zero, and re-arranging for $y = y(x)$ from any of the two equations and substituting it into the other equation, a steady-state solution of the system (2.1) is now written in the form of a reduced singularity function, G [Gray and Roberts, 1988],

$$G(x, \gamma, \mathbf{p}) = 0. \tag{2.2}$$

Using Equation (2.2), various properties of bifurcations such as limit point, cusp, isola, among others can be investigated. A steady-state diagram can be plotted in a graph of x versus γ for fixed $\mathbf{p}$. The objective is to identify the different types of steady-state behaviour and their locations in the bifurcation diagrams, and is discussed in Chapter 5.

Cusp singularity

The cusp singularity is found when G satisfies the conditions

$$G = G_x = G_{xx} = 0\,, \quad \text{with} \quad G_\gamma \neq 0 \quad \text{and} \quad G_{xxx} \neq 0\,. \tag{2.3}$$

When a cusp curve is crossed, the number of limit points (or turning points) on the steady-state curve changes, that is, limit points appear and disappear when moving from one region to the next. The cusp curve splits two regions, one of which has a *hysteresis* feature. Figure 2.2 shows an example of hysteresis which occurs when there are two stable steady-state branches as well as an unstable one between a set of parameters $\gamma_1 < \gamma < \gamma_2$. In this region of γ, the solution approaches one of the two attractors, depending on the starting point, a feature which is an indication of *bistability.*

The occurrence of bistability in population dynamics is not uncommon. For example, Malka et al. [2010] modelled the dynamics of bacterium and phagocyte populations, and found bistability regions that indicate a healthy or an infected state of a host. Elf et al. [2006] studied the response of bacteria to antibiotics, and found bistable behaviour in the bacterial growth rate. Studies by Dubnau and Losick [2006] and Santillán [2008] also discussed bistability. In these studies, the choice of initial conditions has a great impact on establishing a desired or undesired state of the population.

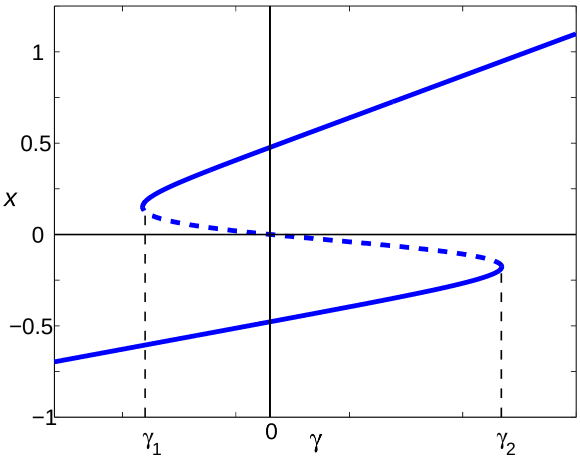


Figure 2.2: A steady-state diagram exhibiting hysteresis behaviour. For $\gamma_1 < \gamma < \gamma_2$, bistability occurs (solid line – stable steady-state, and dashed line – unstable steady-state).

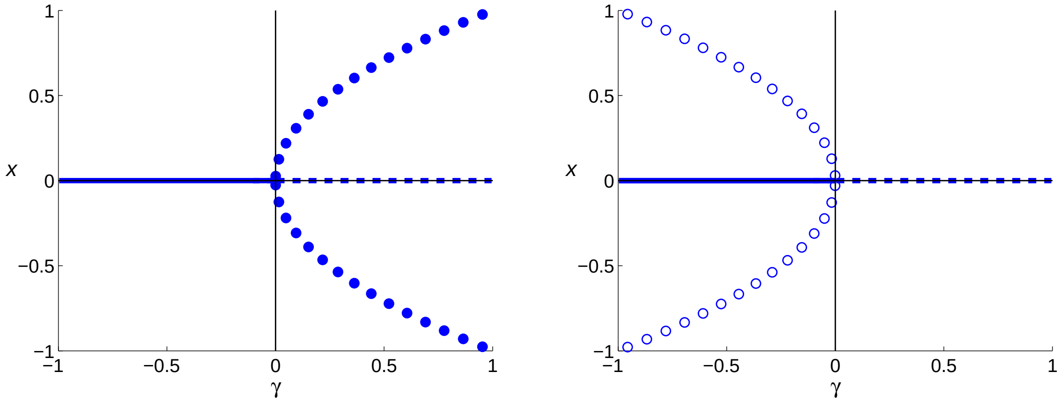
2.1.3 Hopf bifurcation

A Hopf bifurcation occurs when a pair of complex eigenvalues crosses the imaginary axis, and can only arise in a system with two or more equations. It is a local bifurcation that results in a periodic solution branch emanating from an equilibrium point [Kuznetsov, 1998]. The condition for a Hopf bifurcation is the set of $\mathbf{p}$ satisfying

$$f = g = \operatorname{tr}(J) = 0, \quad \frac{d\left[\operatorname{tr}(J)\right]}{d\gamma} \neq 0 \ \text{ and } \ \det(J) > 0,$$

where J is the Jacobian matrix obtained by linearising about the critical points of the system (2.1). A Hopf bifurcation can be either *super–* or *subcritical.* If a stable periodic solution branch emanates from the Hopf point, then the Hopf bifurcation is said to be supercritical (Figure 2.3a). As a result, the system behaviour changes from stationary to a persistent oscillation. Conversely, if an unstable solution branch originates from the Hopf bifurcation, then it is said to be subcritical (Figure 2.3b).

Hopf bifurcations appear in a vast number of ecological applications in which oscillations or periodic phenomena are observed. For example, some predator-prey systems illustrate oscillatory dynamics whereby resource enrichment leads to destabilisation of the system and cause them to switch to limit cycles [Fussmann et al., 2000, Olivares and Palma, 2011].



(a) (b)

Figure 2.3: Types of Hopf bifurcation, (a) supercritical Hopf bifurcation. (b) subcritical Hopf bifurcation (closed circle – stable periodic, and open circle – unstable periodic).

2.1.4 Travelling waves

The standard approach for travelling wave analysis is to convert a PDE problem to an associated ODE system using an appropriate substitution. Analysing the ODE system provides the analytical solution to the original PDE problem. Numerical approach such as the relaxation method is applied to the corresponding ODE system.

Consider a one-dimensional PDE system

$$\frac{\partial u(x,t)}{\partial t} = D_1 \frac{\partial^2 u(x,t)}{\partial x^2} + F_1\big(u(x,t), v(x,t)\big), \tag{2.4a}$$

$$\frac{\partial v(x,t)}{\partial t} = D_2 \frac{\partial^2 v(x,t)}{\partial x^2} + F_2\big(u(x,t), v(x,t)\big), \tag{2.4b}$$

where $u(x,t)$ and $v(x,t)$ are populations with space variable x and time variable t, and D_1 and D_2 the diffusion coefficients of u and v, respectively. F_1 and F_2 are the terms that describe the interactions between u and v.

Let the travelling wave solution have the form $u(x,t) = u(\zeta)$, and $v(x,t) = v(\zeta)$, where $\zeta = x - st$ is a moving frame with speed s. Then, substituting them in system (2.4) and using dimensionless variables gives the corresponding dimensionless ODE formulation

$$\delta u'' + su' + G_1(u,v) = 0, \tag{2.5a}$$

$$v'' + sv' + G_2(u,v) = 0, \tag{2.5b}$$

where δ is the ratio of D_1 and D_2. The functions G_1 and G_2 are the respective transformations of the terms F_1 and F_2. From system (2.5), the steady-states and their stability are investigated. The possible minimum wave speed is generally determined to ensure non-negative solutions, especially when considering population models.

Propagation of travelling population waves has been studied by others [Okubo, 1980, Dunbar, 1983, Murray, 1989, Owen and Lewis, 2001, Huang and Weng, 2013] to investigate how populations disperse spatially. If one species does not move, another species has the advantage if it moves and catches the sedentary population. The waves recognised for this type of situation are sometimes called waves of pursuit and evasion in predator-prey systems.

Relaxation method

Relaxation or collocation is a method to seek solutions for the PDE based on finite-difference schemes [Quarteroni and Valli, 2009], and is an iterative method. Starting with an initial guess, the solution is allowed to "relax" towards the true solution while, at the same time, reducing the errors. We begin with the simplest initial guess function

$$u(\zeta) = \begin{cases} \alpha_1, & \zeta < \zeta_0, \\ \alpha_2, & \zeta > \zeta_0, \end{cases} \qquad v(\zeta) = \begin{cases} \beta_1, & \zeta < \zeta_0, \\ \beta_2, & \zeta > \zeta_0, \end{cases} \tag{2.6}$$

where $u(\zeta)$ and $v(\zeta)$ are step functions. From the governing equations (2.5), the first and second derivatives are discretised using a centered-difference scheme as

$$u' = \frac{u_{n+1} - u_{n-1}}{2h}, \quad u'' = \frac{u_{n+1} - 2u_n + u_{n-1}}{h^2},$$
$$v' = \frac{v_{n+1} - v_{n-1}}{2h}, \quad v'' = \frac{v_{n+1} - 2v_n + v_{n-1}}{h^2},$$

respectively, where h is the step size. Backward- and forward-difference schemes are other options available for discretising the derivatives. We write

$$A = \frac{1}{2h}\begin{bmatrix} 0 & 1 & 0 & & \\ -1 & 0 & 1 & & \\ & \ddots & \ddots & \ddots & \\ & & -1 & 0 & 1 \\ & & & -1 & 0 \end{bmatrix}, \quad B = \frac{1}{h^2}\begin{bmatrix} -2 & 1 & & & \\ 1 & -2 & 1 & & \\ & \ddots & \ddots & \ddots & \\ & & 1 & -2 & 1 \\ & & & 1 & -2 \end{bmatrix},$$

$$H = \begin{bmatrix} H_1 \\ H_2 \end{bmatrix},$$

where A and B are the differentiation matrices , and H is

$$H_1 = \delta B\mathbf{u} + sA\mathbf{u} + G_1(\mathbf{u}, \mathbf{v}), \tag{2.7a}$$

$$H_2 = \ \ B\mathbf{v} + sA\mathbf{v} + G_2(\mathbf{u}, \mathbf{v}), \tag{2.7b}$$

with G_1 and G_2 from the system (2.5). Thus, the vector solution is

$$W_n = \left[\begin{array}{c} u_1 \\ \vdots \\ u_n \\ \hline v_{n+1} \\ \vdots \\ v_{2n} \end{array}\right]$$

such that

$$W_{n+1} = M^{-1}H(W_n),$$

where M is a block diagonal matrix constructed from vectors $\mathbf{u}$ and $\mathbf{v}$. This method is used in Chapter 6 to obtain the travelling wave solution in diffusive population models.

Method of Lines (MOL)

The MOL is a numerical approach to obtaining solutions to PDEs [Schiesser, 1991]. This scheme involves replacing partial derivatives in the spatial variables by finite-difference approximations. As a consequence, only time derivatives are present and as such the PDEs are "converted" to a system of ODEs. Hence all that is required is a good ODE solver such as those available in software packages like MATLAB®, which is discussed in the next section.

In our simulations, the spatial domain is divided into regions with uniform step size. A Neumann boundary condition $\partial u/\partial \mathbf{n} = \partial v/\partial \mathbf{n} = 0$ is used where $\mathbf{n}$ is the outward unit normal vector to the boundary, which reflects the fact that no population can escape across the boundary. Initial conditions are set to be step functions in most simulations. To calculate the wave speed, peaks of the waves are traced for two different time steps. By following the peaks, the speed is calculated by dividing the distance by the time difference between the peaks. This method is applicable for constant speed, since it is easy to trace waves with the same speed. However, to trace waves with non-constant speeds, a more accurate method and careful analysis are needed. In our numerical calculation, we use the algorithm developed by Fornberg [1988, 1998] to generate and compute finite-difference weights at each grid point. The algorithm works for equispaced grids and also for arbitrarily spaced grids.

2.2 Software packages

Mathematical modelling, especially when considering nonlinear systems, is quite challenging. If it is not possible to obtain an analytical solution, numerical analyses must be used for solving complex systems. The following software packages are ones we found useful in this research.

MATLAB®

MATLAB® [MathWorks, 2008] is a powerful computing tool widely used to analyse and explore mathematical models in a huge range of applications. Most of plots in this thesis were made with MATLAB®. Numerical simulations in Chapters 3 and 4, and the steady-state and periodic solutions in Chapter 5 were found and verified using inbuilt MATLAB® ODE solver routines such as ODE15s, ODE23 and ODE45.

ODE45 is based on a fourth/fifth order Runge-Kutta formula. It is a one-step solver, similar to ODE23 [Redfern, 1998, Moler, 2008]. In general, ODE45 is the first solver to be used to solve ODE system before trying other solvers. ODE23 uses the second and third order Runge-Kutta formulas. In most cases, ODE45 is more accurate and more efficient than ODE23. ODE23 is used to solve problems with crude error tolerances or for solving moderately stiff problems. ODE15s is a multi-step solver that solves stiff ODE systems, and is used if ODE45 fails or is found to be inefficient to solve the system.

MATLAB® is capable of solving PDE problems in one, two and three dimensions provided the correct toolbox is available in the package. The spatially dependent models in Chapter 6 were solved using numerical routines such as the finite-difference method and MOL with the algorithms we developed in MATLAB®.

MAPLE

MAPLE [Maplesoft, 2008] is another efficient computing package for analysing mathematical models. Its capability for interactive symbolic computation is very useful and it is able to generate numerical and graphical representations. This software was used for the greater part of the singularity analysis in Chapter 5. Some parts of the analytical work in these chapters were verified using this software, especially the analytical form of the nontrivial eigenvalues of the steady-states.

G3DATA

G3DATA [Frantz, 2000] is a freeware executable tool for extracting data from graphs found in articles. With these extracted data, the plots can be redrawn and further analysis can be done, particularly to compare the analytical solutions with the experimental data. The use of this software is discussed in Chapter 3.

XPPAUT

XPPAUT [Ermentrout, 2010] is a freeware tool for analysing and simulating dynamical systems. This package was found to be extremely useful in obtaining the steady-state plots as well as periodic-solution branches. The stability of the steady-state and of periodic-solution branches are easily determined by XPPAUT's inbuilt AUTO [Doedel, 2007] program which allows for path-following and bifurcation analysis. This software was extensively used in Chapter 5.

FlexPDE™

FlexPDE™ [PDE Solution Inc., 2011] is a script-based numerical solver designed to solve a PDE problem. Although it is a commercial package, a free student version (with restricted mesh size) is also available. We used this software to solve spatially dependent models such as the travelling waves in Chapter 6. Similar to MATLAB®, it is able to solve the PDE problem in one, two and three dimensions through its automatic inbuilt computational technique – adaptive mesh refinement. This method adapts the finite-element mesh in areas with large errors. It iterates the mesh cells and if any exceed this specified tolerance level, FlexPDE™ recomputes the solution. As a result, the accuracy of the solution is guaranteed and errors are minimised to the desired relative error tolerance level. The error tolerance level (`errlim`) depends on the type of the PDE problem. The script codings for the governing equations are easy to write and the graphical output interface allows several plots to be analysed simultaneously while the computations take place. The data can be extracted from the solution and exported to other numerical software for further analysis. As an independent solver for the PDE system, FlexPDE™ can be used as a validation of the solutions obtained via MOL or finite differences.

2.3 Conclusions

This chapter presents the analytical and numerical methods, and software packages used in the analysis in this thesis. In the next chapter, fundamental models are presented and investigated. An application of the model is also discussed and verified.

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