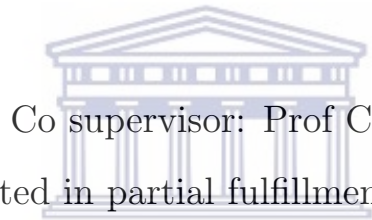


The Paradox of Enrichment in Predator-Prey Systems

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A thesis submitted in partial fulfillment of the requirements

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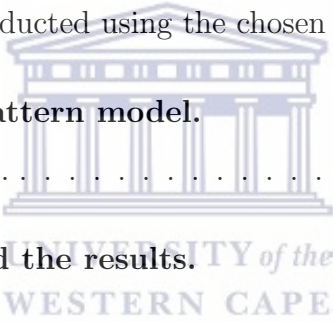
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Declaration

I declare that is my own work, that it has not been submitted for any degree or examination in any other university, and that all the sources I have used or quoted have been indicated and acknowledged by complete references.

Msimelelo Sogoni



26 November, 2020

Signed: 

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Radebe, Bungane, Mthimkhulu, Ngelengele...

Key words

KEYWORDS

enrichment

extinctions

evolution

local stability

Lotka-Volterra equations

Lyapunov stability

paradox of enrichment

partial differential equations

predator-prey

reaction-diffusion

spatial structured patterns

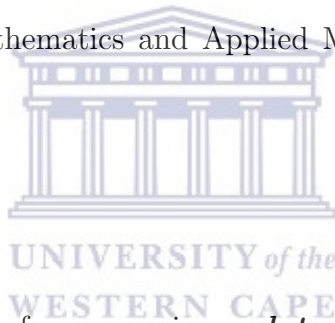


Abstract

THE PARADOX OF ENRICHMENT IN PREDATOR-PREY SYSTEMS

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In principle, an *enrichment* of resources in *predator-prey systems* show prompts destabilisation of a framework, accordingly, falling trophic communication, a phenomenon known to as the “*Paradox of Enrichment*” [54]. After it was first genius postured by *Rosenzweig* [48], various resulting examines, including recently those of *Mougi-Nishimura* [43] as well as that of *Bohannan-Lenski* [8], were completed on this problem over numerous decades. Nonetheless, there has been a universal none acceptance of the “*paradox*” word within an ecological field due to diverse interpretations [51].

In this dissertation, some theoretical exploratory works are being surveyed in line with giving a concise outline proposed responses to the *paradox*. Consequently, a quantity of *diffusion-driven models* in mathematical ecology are evaluated and analysed. Accordingly, piloting the way for the *spatial structured pattern* (we denote it by *SSP*) formation in nonlinear systems of *partial differential equations* [36, 40].

The central point of attention is on *enrichment* consequences which results toward a *paradoxical state*. For this purpose, evaluating a number of compartmental models in ecology similar to those of [48] will be of great assistance. Such displays have greater influence in pattern formations due to diversity in meta-population.

Studying the outcomes of initiating an *enrichment* into [9] of Braverman's model, with a *nutrient* density (denoted by n) and *bacteria* compactness (denoted by b) respectively, suits the purpose. The main objective behind being able to transform [9]'s system (2.16) into a new model as a result of *enrichment*. Accordingly, n has a *logistic-type growth* with *linear diffusion*, while b poses a *Holling Type II* and *nonlinear diffusion* $\nabla^2 \sigma n b^2$ [9, 40].

Five fundamental questions are imposed in order to address and guide the study in accordance with the following sequence:

- (a) What will be the outcomes of introducing enrichment into [9]'s model?
- (b) How will such a process in (i) be done in order to change the system (2.16)'s stability state [50]?
- (c) Whether the *paradox* does exist in a particular situation or not [51]? Lastly,
- (d) If an *absurdity* in (d) does exist, is it reversible [8, 16, 54]?

Based on the problem statement above, the investigation will include various *matlab* simulations. Therefore, being able to give analysis on a *local asymptotic stability* state when a *small perturbation* has been introduced [40]. It is for this reason that a *bifurcation* relevance comes into effect [58]. There are principal definitions that are undertaken as the research evolves around them.

A study of quantitative response is presented in *predator-prey systems* in order to establish its *stability* properties. Due to tradeoffs, there is a great likelihood that the *growth rate*, *attack abilities* and *defense capacities* of species have to be examined in line with reviewing parameters which favor *stability* conditions. Accordingly, an investigation must also reflect chances that leads to *extinction* or *coexistence* [7].

Nature is much more complex than scientific models and laboratories [39]. Therefore, different mechanisms have to be integrated in order to establish *stability* even when a system has been under *enrichment* [51]. As a result, *SSP* system is modeled by way of *reaction-diffusion differential equations* simulated both spatially and temporally. The outcomes of such a system will be best suitable for real-world life situations which control similar behaviors in the future. Comparable models are used in the main compilation phase of dissertation and truly reflected in the literature. The *SSP* model can be regarded as between (2018-2011), with a *stability control* study which is of an original.



List of Acronyms

MS means matlab simulator

PoE means paradox of enrichment

SSP means spatial structured pattern.



List of notations

$\xi(M)$ represent the *index of enrichment*.



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Chapter 1

General Introduction

The so-called *Paradox of Enrichment* has assumed an imperative component within species interaction resulting in transforming science of technology into a succession of paradigms [39]. After *Rosenzweig's* [48] discovery which described the outcomes in six predator-prey models, *Roy-Chattopadhyay* [51] stated that, “wherein increasing food availability to the prey would cause the predator’s population to destabilise”. Equally, [48] used an application of ordinary differential equations to simulate *predator-prey* interactions.

Definition 1.0.1. The *Paradox of Enrichment* basically implies that if a supplement has been included in an environment with at least two or more connecting populations, with the real result of moving such a framework towards an unsteady state, bringing about uneven characters that thusly prompts termination of the species included [54].

Both in ecological and biological context, this means that increasing food available to an ecosystem leads to *instability* [57]. Other ending results can be *extinction*, since improving or enhancing the carrying capacity of a species notionally destabilises *predator-prey dynamics* as far as mathematical ecology is concerned [48].

Regulation of population depends upon both the *bottom-up* and *top-down* forces [58]. The major role players according to earliest view being the primary producers, an efficiency of energy and an upward intake of material across trophic levels [36].

Consequently, a construction of an ecological ecosystem had been influenced by these views mentioned above, which holds for apex predators having a minor authority on environmental functionality [51, 48].

Only around the mid 1960s that a focus on species interaction changed drastically to competition [53]. The only major challenge with this approach was that all species within trophic levels had an equivalent cause not only just predators [26]. In new research developments, *top-down* procedures have again reflected the importance of predators resulting directly to spatial structured patterns (we shall refer to it as *SSP*) formulation [39]. The emphasis is more on *top-down forces* created by ***apex predators***. Notwithstanding, biodiversity requires more species interaction than *bottom-up* versus *top-down techniques* [3].

Mathematical modeling of both qualitative and quantitative developments in *predator-prey dynamics* plays a significant role in controlling biodiversity and coexistence [2]. It is crucially along these lines that accurate representation does give a clarity on assumptions to be used, variables and parameters to be considered. As the main focus is more on *diffusion-driven predator-prey systems*, a review and recognition of the previous work done so far in line with the *paradox's* evolution is highly significant.

Interaction of various species in the field of ecology, mathematical modeling and two dimensional *spatial structured pattern* formations had drawn much attention, especially within the scientific research field and policy formulation processes [16]. In any case, extraordinary outcomes of such interactions depend entirely on both the suitability and character of species involved [36]. For example, reproductive rate and food intake supplements have a direct influence on how patterns will be formed [50, 19]. It is for this reason that the word “*enrichment*” in interacting *predator-prey dynamics* is of pertinent.

Definition 1.0.2. The term ***enrichment*** both in a biological and environmental context has been utilised as meaning “an enhancement of species’ physical or social encompassing environment [8, 27], successively to progress behavioral effects” [10].

Example 1.0.3. Let us consider an interaction of two populations, being a *bacteria* (predator) and its *nutrient* (prey) [16]. *Bacteria* depends entirely on the presence of its *nutrient* for it to survive [20].

Based on this dependency, in the absence of its *nutrient*, *bacteria* will therefore die eventually [37]. Equally, the case would totally be different when there is no *bacteria* as it could enable its *nutrient* to grow and increase its density without any disturbance [8]. The *nutrient* population decline might be associated with its normal death or other external factors [28]. Interestingly, is “what then occurs in the presence of both species?”

Alternatively, the *Paradox of Enrichment* evolves as a result of a *consumer-resource system* assumption with the *predator’s vertical isocline* presence being able to link trophic levels and the *prey-dependent functional response* [48, 59]. This occurs as the *predator’s functional response* is directly influenced by the prey’s abundance instead of consumers within a *prey-dependent system* (the situation being that of *Lotka-Volterra* [54, 8]). In an instance of a *predator-dependent system*, the carrying capacity at which destabilisation takes place increases as is interference [7].

Subsequently, models of *Beddington-DeAngelis*, *Hassell-Varley-Holling* together with that of *Arditi-Ginzburg* are being considered. Despite the fact that a lot of work has been done towards [48]’s paradox, an original logistic equation (2.3) had been utilised as a key fundamental component of population growth in *predator-prey theory*. Pioneers in those circumstances, incorporate amongst others, a **Thomas Malthus**’s “*essay on the principle of population*”. This was shortly transformed by *Peirri Verhulst* [12] into a *mathematical logistic equation* and later followed by the modifications of *Pearl-Reed* [25]. Afterward, in *Veilleux*’s experimental work [30], an *enrichment* resulted in increasing both the growth rate and carrying capacity concurrently [33, 36].

1.1 Biological background

In ecological principles, the concept of *enrichment* had been widely debated [39, 19]. It has been shown to play a significant role around environmental structures and probably

some behavioral patterns [5]. A well-defined meaning of the *Paradox of Enrichment* under **Definition** (1.0.1) is therefore very crucial and also significant as it elaborates further on some research done so far. This will enable us to extract gaps that successively will assist in bridging biological data with mathematical modeling.

To give a brief summary with regard to the *Paradox of Enrichment's* evolution, a reference to the flow chart diagram in Figure 1.1:

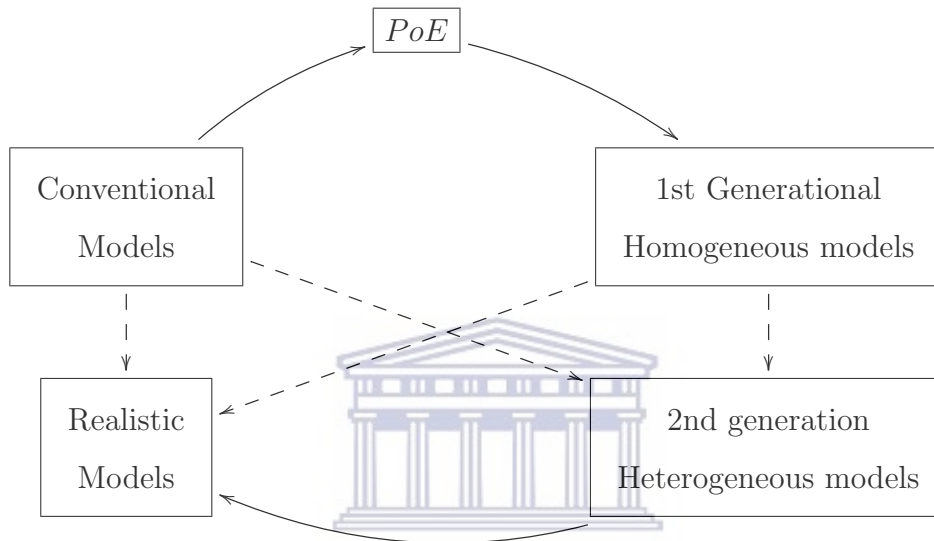


Figure 1.1: The flow chart diagram representing the *PoE's* evolution.

1.2 Ecological and mathematical models normally used to investigate the paradox.

The most commonly used models to the *Paradox of Enrichment's* study include, amongst others, a *Levins* conventional system and those of *Huffaker et al* [7]. Currently, displays of *Holt-Polis* and *Rosenzweig-McArthur* take a core central lead [40]. Equally, the **second-generation models** (as illustrated in Figure 1.1) which mostly supported *Rosenzweig's paradox* theory, are also used in more realistic approaches in recent times and for future purposes [15]. Likewise, a serious discrepancy between theoretical expectations and observations on natural *predator-prey dynamics* prompted investigators to propose

a number of abstract mechanisms for the *paradox's* resolution [12, 31]. These includes, amongst others, the following accompanying factors:

(i) The ***presence of an inedible prey*** had been developed as a general class of mechanism by expanding the original *Roseinzweig-McArthur model* [43]. According to *Murray* [39], with its clear role being to clarify disparities between the theory and observations. A common division was made by *Roy-Chattohadhyay* [51] on the assumption that a prey class consists of two types of species only, one that is ***edible*** to the predator and another, being ***inedible***. The effects of a *neutral inedible prey*, *interfering inedible prey* and *nutritionally valueless prey* were shown in a detailed theoretical analysis study of *Kawasaki et al.* [31] as to be a resolution to the *Paradox of Enrichment* [32].

A different view which emerged in *Rohani et al.* [50] was additionally raised with a *neutrally inedible prey* generally not being consumed by the predator. As a result, it directly influenced interactions between the predator and its *edible prey* [54, 32]. An *inedible prey* thus, exerted control over the *edible producer's nutrient* content. It had been shown in different studies of *Kawasaki et al.*, *Murray*, *Mougi-Nishimura* [31, 40, 42] that the presence of such an *inedible prey* overturned destabilisation due to *nutrient's enrichment* [43]. Experimental work of [51] also established that the presence of an *inedible prey* acting as a *nutrient sponge* provided a plausible mechanism to resolve an *ecosystem enrichment's* paradoxical outcome [12, 31, 40].

(ii) The ***presence of an invulnerable prey*** as *Vos et al.* [54] mentioned, is a result due to several reasons, namely:

(1) That some individuals among the prey population would appear to the predator in a transitional state between the vulnerable and invulnerable classes [54].

(2) An invulnerability of an individual prey might either be due to its physiological and behavioral state or its spatial location [31].

(3) In some situations, predators could not gain access due to a *selective occupational spatial location* of immobile prey, resulting in reducing predatory risks as an individual prey would be invulnerable [32].

Incorporating such a *predator-prey system* in a dynamic class of a prey population

that is invulnerable due to spatial location had greatly reduced the prey's vulnerability to predators based on some potential survival activity associated with their physiology [43, 12, 31].

It was further shown in [51]'s study that, *enrichment* did not destabilise *predator-prey dynamics*. Instead, it only supplementary enhanced its *steady state* [12]. Hence, *Bontje et al.* [32] argued that, when a *predator-prey system* consisting of an *invulnerable prey class* had been enriched, the result was a direct increase in their population numbers. Consequently, that brought about an enhancement in the biomass of the entire prey's population [41].

Nevertheless, sequentially resulted in boosting an input of individuals in a *vulnerable class* by changing the *predator-prey interactions* to a “*donor-controlled system*” [22]. The dynamics of such a system had been shown to be strongly stabilising [15, 32, 12]. *Jensen-Ginzburg's* experimental work supported such previous theoretical analysis [30] by showing that an *invulnerable prey* stabilised the trophic level dynamics as replacing more *vulnerable preys* (similar views that also gained support in [35, 32]).

(iii) The ***presence of the unpalatable prey*** separately from a class of a *profitable edible* and an *inedible prey* within the *enrichment context* in *predator-prey theory* had emphasised the presence of another prey class which is *less profitable* but *edible* [32]. The profitability of such preys emerged to be lower than a *certain critical value* even if they were to be consumed at a high biomass and a *predator nutritional requirement* would be unfulfilled [42]. Based on *Kato-Yamamura* [16]'s system (2.13) findings, such preys are referred to as “***unpalatable***”. Occurrence of an *unpalatable prey* where a predator exhibited *optimal selective feeding* resulted in an amplitude reduction of dynamic oscillations due to *enrichment* [54, 16].

Moreover, an *unpalatable prey* in an enriched *predator-prey ecosystems* prevented a minimum abundance of species from falling below certain values, resulting in robustness boost of *stability* against *enrichment* [59, 58]. Subsequently, the findings of *Genkai-Yamamura* [16] concluded that a profitability of an *unpalatable prey* had a vast potential to act as a key predictor for a dynamic behavior of any *predator-prey system* in

nature [5]. Research experiments of [32] have shown that due to physical and biological constraints,

the quality of food in both planktonic and terrestrial ecosystems sometimes decrease at a high biomass.

Quite recently, [51]’s study proposed a simple phenomenological relationship to describe an *energy degradation value* at increased levels of a carrying capacity. Subsequently, [51]’s discovery showed that an incorporation of a proposed relationship in a simple *predator-prey model* overturned destabilisation possibility of community dynamics due to *enrichment* by theoretical analysis. It was then, further assumed that the trophic function depended on a *bacteria:nutrient* ratio abundance [43, 12].

Definition 1.2.1. A *ratio-dependent functional response* in a *predator-prey* system means the *functional responses* which are fully dependent on the prey’s density [57].

(iv) A *ratio-dependent functional response* was based on a number of empirical observations conducted previously by the likes of *Courbau et al.* [7], which had consistently supported the argument of [51] as a *trophic function*. With the incorporation of such systems to an *uptake function*, [51] showed that *enriched dynamics* having an *oscillatory instability* with a carrying capacity remained unchanged [57]. As a result, such interaction systems could not rise to a simple *predator-prey model* [2].

Conversely, due to inappropriateness of such systems, a proposal by *Kawasaki et al.* [31] was made, that, considering the time scale of population dynamics on which models operate differed from behavioral patterns. Consequently, [51] recommended that the uptake function is termed a *ratio-dependent functional response*. An argument that received a number of support among empirical observation studies recently [43, 12].

(v) A *spatial interaction* or *spatio-temporal chaos* enabled ecologists and researchers at large to study the effects of both space and time in interacting species [50]. Afterward, *Jansen* [27] extended the scope of a simple *Lotka-Volterra* and *Roseinzweig-McArthur model* in a patchy environment with closer focus being to

interpret the formation of patterns. The result analysis of both [31] and *Pimms et al.* [46] correspondingly, demonstrated that spatial interactions caused fluctuations of *predator-prey dynamics* and regulated its population abundance thereof [32].

Moreover, laboratory experiments of [54], [51], [52] and [27]’s theoretical work, also confirmed that spatial patches protect *predator-prey systems* from collapsing due to *population extinction* after *enrichment*. Using a standard *reaction-diffusion system* with a cutoff at low population densities, it was further demonstrated theoretically that a transition to *spatio-temporal chaos* prevented species extinction in an *enriched ecosystem* [54].

Thus, consideration of time and space might efficiently alter the paradoxical outcome of regular dynamics predicted by simple *predator-prey models* [58]. In [54]’s investigation, many ecological studies conducted thereafter presented methods which promoted or destroyed population stability. Consequently, [54] analysed models of *bi* and *tri-trophic* food chains that incorporated *consumer-induced polymorphism*.

(vi) **Induced defenses**, according to *Xu-Li* [58] have also been shown to decelerate a rapid population decline of *Daphnia* under peak fish predation. That contributed to persistence of prey-populations in the face of high predation risk by efficient predators. Experimental work of [51] further demonstrated that at high population density *Rotifers* produced some unidentified auto-toxin that acted as a source of *density-dependent predator mortality*. Consequently, the predator’s death rate increased in direct response to an increase in its biomass [5, 42].

Later on, results in [54] have shown that *intra-species heterogeneity* in defense levels overturned *instability* subsequently to *enrichment*. Essentially to that, *inducible defenses* represented a *predator-dependent result* with an indirect interference [57]. Although the outcomes were found to be caused by differences in handling times, conversion rate, efficiencies between defended and undefended prey, it was later also discovered that a *stabilising result* in [54] remained unchanged even if *inducible defenses* affected the consumer’s attack rate. *Inducible defenses* promoted persistence of *predator-prey species* in *tri-trophic* food chains by bounding the minimum abundance of population from falling

below a minimum value [32].

(vii) A *density-dependent predator mortality* had been shown to alleviate *predator-prey dynamics* as its introduction theoretically provided a *stabilising effect* within *enrichment* [41, 24]. In [51]’s discussion, a conclusion had been drawn that such a *stability*, using a *predator-prey model* with a *Holling Type II functional response* were similar to those of Braverman’s (2.16) display [9, 58, 59]. Based on observational results then, [51] showed that *density-dependent predators* could also for some other reasons be able to stabilise *predator-prey dynamics* [40, 32].

A relatively case to consider was that of the Daphnia algal system, in which other predators switched to a preferred diet in the absence of their preys’ specialised choice [51, 58]. As a consequence of that, consideration of *density-dependent predators* might then be reasonably adequate in simple *predator-prey models* [5, 12, 32].

As more research interest developed, many ecologists started an investigation towards the *paradox*’s resolution [51].



1.3 Biological applications of the *Paradox of Enrichment* and its ecological importance.

Quite recently, the *Paradox of Enrichment*’s relevance in aquaculture production has been highly recognised (in the research work of [32, 31] and reference therein) for its vital fundamental role it plays globally in food demand. The *Paradox of Enrichment* is applied to establish an *ecosystem’s biodiversity* and *continuous productivity* in order to enhance *stability* within population dynamics [59, 58].

In turn, *biodiversity* has a huge economical value chain in representing environmental cultural heritage [46]. The *Paradox of Enrichment* plays a significant role in *competition colonisation trade-off* as it is considered to be an important mechanism explaining *coexistence* in *spatial structured pattern* environments [7, 25].

There has been a significant role of applying the *Paradox of Enrichment* in *ecosystem*

conservation management along with an *invasion control system* of species [19]. Both in *ecosystem restoration* and *pest management control*, respectively, the *Paradox of Enrichment* has been widely applied. In *natural resource exploitation* which includes amongst others hunting, fishing and forestry, the *Paradox of Enrichment* had been functional practical [57]. In cases where spatial distribution of two or more population is of interest, a passive dispersal had been modeled by the use of a *diffusion-operator* [19, 26].

Other ecological importance of the *Paradox of Enrichment* includes amongst others the following:

- (i) A total maximum removal value on both the number and the weight harvest of species [44, 47].
- (ii) In age, sex and restriction of certain individuals within a harvested species [37].
- (iii) In closed exploitation area boundaries on where individuals can be harvested [46].
- (iv) In a fixed exploitation seasonal limit on when individual members of a species can be harvested [40, 47, 43]. This strategy is often employed for both *species management* and *recreational purposes* respectively.
- (v) In *predator control-culling* population to enhance prey inhabitants.
- (vi) In *prey control-culling* of competitive species to enhance population of a specific species.
- (vii) In *prey enhancement-support* on environmental changes to enhance harvest of a desired species.

1.4 Descriptions of chapters

The rest of the thesis is composed as follows:

In chapter 2, biological and mathematical preliminaries are introduced as basic fundamental important prerequisites to the *Paradox of Enrichment* study in *predator-prey dynamics*. Systematically organised to familiarise the reader with definitions in addition to the methods used in *spatial structured pattern* models. The remaining part provides

literature review.

Firstly, representing the *Paradox of Enrichment's* evolution alongside mathematical models which are reflecting a key cornerstone of prevention, control and also providing a direction on an analytical interpretation of ecological invasion [19]. An assessment focuses on some previous work done regarding the *Paradox of Enrichment*, taking into consideration the relevance of *Braverman* [9]'s system (2.16) as a *spatially structured pattern's* system (3.1) formulation foundation.

Stability analysis and *bifurcation* of various models are also evaluated together with the use of a *matlab simulator* in modeling [58, 11]. The outcome of this consideration result in strongest justification of model (3.1) as a choice through which a gap analysis along the *paradox* are represented.

In chapter 3, a model (3.1) has been developed by first taking into consideration [9]'s system (2.16), which focused on a *spatial homogeneous system* with three different points of equilibrium. Thereafter, the next step involves performing a *stability analysis* and some numerical results for each of the three cases presented [50]. An introduction of a small perturbation into [9]'s system (2.16) with few parameter adjustments to fit the new model environment.

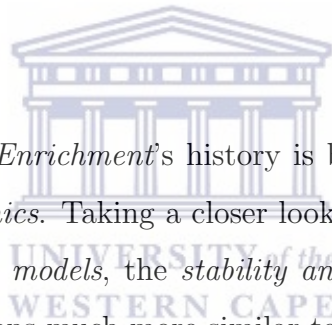
A simulation process has then being dealt with in chapter 4 by taking into account different forms of interactions and possible likelihoods for future behavior. An investigative gap plan is used as a benchmark to define the model and its strength. Points of common interest have been put as a yardstick, while challenges opened for further testing the model against all various environmental forms.

Furthermore, chapter 4 deals specifically with acquired results from the previous work. Some of these results will be used for further publication in future. The last chapter incorporates conclusion and a way forward.

Chapter 2

Literature review and preliminaries

2.1 Introduction



In this chapter, the *Paradox of Enrichment's* history is briefly evaluated along with its evolution in *predator-prey dynamics*. Taking a closer look into both *spatial homogeneous systems* as well as *heterogeneous models*, the *stability analysis* has been reviewed along with *matlab simulation* applications much more similar to those of *Colasanti* [11] in ecological modeling.

An assessment will further include the diffusion's role and *enrichment* in mathematical modeling. In addition, various strengths and weaknesses of other models reviewed so far are highlighted. History of *predator-prey dynamics* with analytical methods and ecological interpretations will also be evaluated [58, 19, 39].

Based on this reason mentioned above, future physiological behaviors and new parameters can be drawn from *predator-prey classes* in order to address a *paradoxical state* [59]. An *optimal control strategy* has been included as part a mathematical analysis [16]. An investigative consideration will further give some details in the historical background of using a *bifurcation theory* in *predator-prey systems* [40]. Ecological basic surroundings are also conducted on other models describing similar two or more

interacting populations [50].

2.2 Preliminaries.

The main purpose of this section is to briefly examine some several definitions, methods, theorems and lastly outcomes that are essential mathematical prerequisites to an ecological study in general. Therefore, this section serves merely as a diminutive outline and suitable reference.

Consequently, some mathematical explanations are incorporated together with ecological definitions. Further useful reference in this regard is a *Jordan et al.*'s book [29], which explicitly reflects behavioral change effects as a result of population interactions [50, 40].

Definition 2.2.1. An *Eden model* is a lattice pattern replica for the growth of cell colonies which forms *tumor-like* structures with *finger-like projections*.

Remark 2.2.2. All neighbors of an active cluster (in Definition 2.2.1) at any given time form a growth zone randomly, with a new point to be attached chosen amongst other neighbors. A reference therein to *Molchanov* [38] for structural diagrams.

Definition 2.2.3. A *dense-branching morphology* is characterised on account of its *circular* envelope modulated by leading branch tips with diffusion controlled cell growth.

Definition 2.2.4. A *ballistic aggregation* is a model whereby new particles move along straight lines (referred to as *ballistic trajectories*) until they hit the cluster or disappear completely, leaving a window of observation.

If a mobile (flying) particle contacts the growing cluster in *ballistic aggregation*, it sticks at any point with its first touch.

Remark 2.2.5. Let a system of ordinary differential equations with its associated nonlinear structure be defined by:

$$\dot{\bar{x}} = f(x) \text{ and } \dot{\bar{y}} = Ay$$

respectively, with the matrix $A = Df(x)$ in the neighborhood of a point $x_0 \in \mathbb{R}^n$.

Definition 2.2.6. For all $f(x_0) = 0$, $x_0 \in \mathbb{R}^n$ is called an *equilibrium point* or a *critical point* of the system under Remark 2.2.5.

Definition 2.2.7. If none eigenvalues of the matrix $Df(x_0)$ have zero real part, then $x_0 \in \mathbb{R}^n$ is called a *hyperbolic equilibrium point*.

Definition 2.2.8. Let $V : \mathbb{R}^n \rightarrow \mathbb{R}$ be a continuous scalar function. Then, V is a *Lyapunov function* at a point 0 if it is a *locally positive-definite* function (meaning $V(0) = 0$ and $V(x) > 0$ for all $x \in U\{0\}$ for some U of 0).

Definition 2.2.9. Let $x^*(t)$ be a given real or complex solution of a system. $x^*(t)$ is *Lyapunov stable* on $t \geq t_0$ if, for any $\epsilon > 0$, there exist $\delta(\epsilon, t_0)$ such that for a solution $x(t)$: $\|x(t_0) - x^*(t_0)\| < \delta \Rightarrow \|x(t) - x^*(t)\| < \epsilon$ for all $t \geq t_0$.

Remark 2.2.10. Otherwise, $x^*(t)$ is said to be *unstable*. An observation had been made by [29] that, if an order is satisfied for initial conditions at t_0 , then a similar state holds when $t_1 > t_0$ is substituted for t_0 . That is, if $x^*(t)$ is stable for $t \geq t_0$, it is also stable for $t \geq t_1 > t_0$.

Definition 2.2.11. If a solution is stable for $t \geq t_0$ and δ is independent of t_0 , then it is said to be *uniformly stable* on an interval $t \in [t_0, \infty)$.

Definition 2.2.12. Let x^* be a stable or (*uniformly stable*) solution for $t \geq t_0$. If there exist $\eta(t_0) > 0$ such that $|x(t_0) - x^*(t_0)| \leq \eta$ is fulfilled whenever $\lim_{t \rightarrow \infty} |x(t) - x^*(t)| = 0$, then x^* is said to be *asymptotically stable*.

Remark 2.2.13. Solutions of a system in the form $\dot{x} = f(x)$ are particularly significant in ecology.

Theorem 2.2.14. Let A be a constant matrix of a system $\dot{x} = Ax$ having eigenvalues $\lambda_i = 1, 2, \dots, n$.

(i) A is *stable* whenever $\operatorname{Re}\lambda_i \leq 0$ for all $i = 1, 2, \dots, n$.

(ii) A is *uniformly stable* when either $\operatorname{Re}\lambda_i < 0$ for all $i = 1, 2, \dots, n$. or $\operatorname{Re}\lambda_i \leq 0$ for all $i = 1, 2, \dots, n$, without any zero repeated eigenvalues.

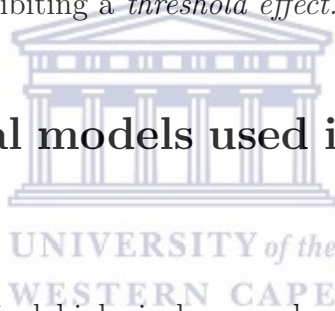
(iii) A is *asymptotically stable* whenever $\operatorname{Re}\lambda_i < 0$ for all $i = 1, 2, \dots, n$.

(which guarantees *uniformly stable* by (ii)).

For the proof a reference to *Hirsh-Smale's* book therein [22].

Remark 2.2.15. In the threshold phenomena, *Murray* [39] discussed a group of interesting models which have a *nonzero stable state*. If perturbation on the threshold is sufficiently large or of the right kind, population densities undergo large variations before returning to steady state, exhibiting a *threshold effect*.

2.3 Mathematical models used in the Paradox of Enrichment.



A significant part of theoretical biological research earlier on had addressed a reality that interactions are more than random encounters [50]. A system of *partial differential equations* has been used in the past decades to model *predator-prey* interactions since *Lotka-Volterra's* pioneering work (see *Holmes et al.* [19]). Likewise, a presentation is done for three classes around the *Paradox of Enrichment's* evolution based on previous work done.

(1) **Conventional models** played a significant role by ensuring that the *Paradox of Enrichment* had captured innumerable ecologists [30]. Consequently, *Rosenzweig* [48]'s view had been widely upheld as a classic instance of an ecological *paradox* ever since its discovery. Simultaneously, *Rosenzweig-MacArthur* [47]'s work had been highly influenced by the pioneering work of *Lotka* [51] and *Ginzburg* discretely [30, 40]. However, [48] used the word "*paradox*" to express an apparently contradictory role of *enrichment* in

ecosystems.

The original *Lotka-Volterra* model [47]:

$$\begin{aligned}\frac{dx}{dt} &= rx\left(1 - \frac{x}{K}\right) - mxy, \\ \frac{dy}{dt} &= emxy - \delta y\end{aligned}\tag{2.1}$$

had been broadly studied in [48, 49, 9, 18, 6, 23] and references therein. Variables $x(t)$ and $y(t)$ being densities of the prey and predator respectively at time t [58]. Parameters of system (2.1) being given by:

r as an intrinsic rate of a prey population increase,

m as a predation rate coefficient,

K as the environment's carrying capacity. Lastly,

δy being a predation mortality rate.

Later on according to Roy-Chattopadhyay [51], system (2.1) was modified by [47] to include a *logistic growth* for the prey and a *functional response* for its predator. It then took the following form of equations:

$$\begin{aligned}\frac{dx}{dt} &= g(x) - f(x)y, \\ \frac{dy}{dt} &= \epsilon f(x)y - my.\end{aligned}\tag{2.2}$$

System of equations (2.2) above had been generally studied in [48, 49, 31, 32] and references therein.

Remark 2.3.1. Let the parameters of an interacting *predator-prey system* be defined by:

x denotes the prey density,

a represents the predator's attack rate (or searching efficiency),

T_{tot} represents the total time spent,

T_{s} represents the total search time,

T_{h} represents the handling time per prey, and lastly

C_{r} represents the prey's consumption rate.

Then:

Definition 2.3.2. *Holling Type I* is given by the system of equations $C_r = aT_s x$.

Noticeable is that \mathbf{T}_s decreases as prey numbers increased. Thus, \mathbf{T}_s is not a constant and therefore will keep on changing. With parameters kept the same as in Remark 2.3.1:

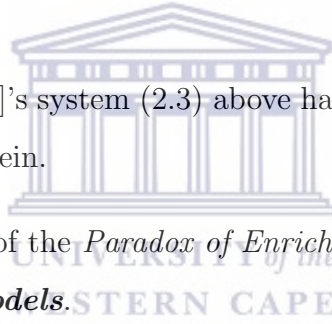
Definition 2.3.3. Let $T_s = T_{tot} - T_h C_r$ denote a difference between total time spent and the product of handling time together with consumption rate. Then, $C_r = \frac{axT_{tot}}{1+aT_h x}$ is called a *Holling Type II functional response*.

Thus, with the persuasion of *Huffaker* [54], *Rosenzweig's paradox* popular model (2.3) [48]:

$$\begin{aligned}\frac{dV}{dt} &= rV\left(1 - \frac{V}{K}\right) - kP(1 - e^{-cV}), \\ \frac{dP}{dt} &= AkP(e^{-cJ} - e^{-cV})\end{aligned}\tag{2.3}$$

was established.

Remark 2.3.4. Likewise, [48]'s system (2.3) above had been broadly extensively studied in [48, 49] and references therein.



Later on, other examples of the *Paradox of Enrichment* included the following:

(2) The **1st generation models**.

(i) An extension of *Tilman's competition model* [53] took the form:

$$\begin{aligned}\frac{dR_1}{dt} &= a_1(S_1 - R_1), \\ \frac{dR_2}{dt} &= a_2(S_2 - R_2).\end{aligned}\tag{2.4}$$

Parameters of [53]'s system (2.4) being given as:

\mathbf{a}_1 and \mathbf{a}_2 representing rate constants,

\mathbf{R}_1 and \mathbf{R}_2 are environmental availabilities of resources. Lastly,

\mathbf{S}_1 and \mathbf{S}_2 standing for maximal amounts of all forms of each resource within a given habitat.

Accordingly, [53]'s system (2.4) therefore accounts explicitly for resources as highly illustrated by the given parameters above.

(ii) A consideration that interactions may be of a mixed type, such as in case of an *intraguild predation* [50], *Pimm et al.*'s model [46] therefore, took the form:

$$\frac{dX_j}{dt} = X_j(b_j + \sum_{i=1}^n a_{ij}X_i). \quad (2.5)$$

Parameters of [46]'s system (2.5) being defined as follow:

X_j being a population size,

b_i as an instantaneous rate of growth with regard to the *ith* species, and

a_{ij} as a per capita effect of the *jth* species on the *ith* species.

This was followed shortly by the discovery of *Holt's intraguild predation* model [20]:

$$\begin{aligned} \frac{dP}{dt} &= P f_P(R, R_P) + g_P[\alpha(P, N, R)N], \\ \frac{dN}{dt} &= N[f_N(R, R_N) - \alpha(P, N, R)P]. \end{aligned} \quad (2.6)$$

Definition 2.3.5. An *intraguild predation* is when one predator preys on another that it competes with for a common resource at different trophic levels.

In [20]'s system (2.6) with such interactions, $\frac{dP}{dt}$ represents an *intraguild predator* while $\frac{dN}{dt}$ represents an *intraguild prey* respectively [20]. Parameters are defined as follow:

f is the growth rate of each consumer on a shared density \mathbf{R} and exclusive resources (at densities \mathbf{R}_N together with \mathbf{R}_P respectively),

α is the death rate of each *intraguild prey* as a result of an *intraguild predator*, and lastly

g_P is the *intraguild predator's* growth rate from consumption.

(3) The **2nd generation models** included:

(iii) An incorporation of behavior into population dynamics [52].

(iv) A recognition that distribution of populations are never *spatial homogeneous* over space and ecological interactions but are modified by *spatial structured patterns* [50].

The discovery mentioned in (iv) gave rise to a broad field of *meta-population theory* and *spatially structured models* cooperatively [6]. This had also influenced *Braverman's* [9] work over that of *Lotka-Volterra*, *Roseinzweig-McArthur*, *Rosenzweig* and others, as it utilised *stability analysis* for a *spatial heterogeneous system* [58, 57, 60].

Along lines of development, *Arditi-Ginzburg* [2] modified systems (2.1-2.6), as they all fell short in satisfying condition (iii) of the *paradox* (reference herein given to Haque [18] for details of the analysis). This was based on the fact that consumers do not normally compete with each other for the same prey. Accordingly, that led to the discovery of a *classical prey-dependent predator* model [2]:

$$\begin{aligned}\frac{dx}{dt} &= rx\left(1 - \frac{x}{k}\right) - \frac{mxy}{ax + c}, \\ \frac{dy}{dt} &= \frac{emxy}{ax + c} - \delta y.\end{aligned}\tag{2.7}$$

The *Holling Type II functional response* system (2.7) had been short-lived as *Arditi-Ginzburg* proposed that a *ratio-dependent functional response* was more suitable in respect to

increasing biological and physiological facts. This was seen possible in cases where predators had a highly competitive searching ability [18]. Afterward, further developments then led to the discovery of *Arditi et al.*'s model [3]:

$$\begin{aligned}\frac{dx}{dt} &= rx\left(1 - \frac{x}{k}\right) - \frac{mxy}{ax + by} \\ \frac{dy}{dt} &= \frac{emxy}{ax + by} - \delta y.\end{aligned}\tag{2.8}$$

The model (2.8) is quite similar to a system (2.7), with only one exception that a constant c had been replaced with $-by$. With an introduction of *intra-species competition* in predator population later on, *Pieluo* [45] customised model (2.1) to take the form:

$$\begin{aligned}\frac{dx}{dt} &= rx\left(1 - \frac{x}{k}\right) - mxy \\ \frac{dy}{dt} &= emxy - \delta y - hy^2.\end{aligned}\tag{2.9}$$

Alternatively, *Bazykin et al.* [5] modified system (2.7) to take the form:

$$\begin{aligned}\frac{dx}{dt} &= rx\left(1 - \frac{x}{k}\right) - \frac{mxy}{ax + c}, \\ \frac{dy}{dt} &= \frac{emxy}{ax + c} - \delta y - hy^2.\end{aligned}\tag{2.10}$$

Further developments afterward carried out by [5] shortly led to the discovery of a *ratio-dependent functional response* system. As a result, *Haque* [18]’s system (2.11) of equations took the following form:

$$\begin{aligned}\frac{dx}{dt} &= rx\left(1 - \frac{x}{k}\right) - \frac{mxy}{ax + by}, \\ \frac{dy}{dt} &= \frac{emxy}{ax + by} - \delta y - hy^2.\end{aligned}\tag{2.11}$$

The *Beddington-DeAngelis* model: As lot of attention was given to *Rosenzweig*’s [48] *paradox* work, it was further extended by *DeAngelis* with an introduction of a supplementary “*functional response*” model in *classical predator-prey* theory.

Beddington-DeAngelis [6] also extended system (2.10) by illustrating parasite host interactions with a set of equations:

$$\begin{aligned}\frac{dx}{dt} &= rx\left(1 - \frac{x}{K}\right) - \frac{mxy}{ax + by + c}, \\ \frac{dy}{dt} &= \frac{emxy}{ax + by + c} - \delta y - hy^2.\end{aligned}\tag{2.12}$$

Variables of the model (2.12) above being $\mathbf{x}(t)$ and $\mathbf{y}(t)$ representing the prey and predator’s densities respectively at time t . Parameters are thus given by:

r as a positive constant for the prey intrinsic growth rate,

K as an environmental carrying capacity,

m as the predator’s consumption rate,

a and c as the prey’s saturation constants,

b as the predator interference,

e as the conversion rate,

d as the predator death rate. Lastly,

h being the predator’s intra-species competition [6].

Quite interestingly, is the development of a simple *Beddington-DeAngelis* model which excluded *intra-species competition*. Thus, allowing $h = 0$ and taking the form:

$$\begin{aligned}\frac{dx}{dt} &= rx\left(1 - \frac{x}{K}\right) - \frac{mxy}{ax + by + c}, \\ \frac{dy}{dt} &= \frac{emxy}{ax + by + c} - \delta y.\end{aligned}\tag{2.13}$$

All above-mentioned models have been extensively applied towards a *predator-prey interaction* study, with more focus on improving understanding of the *Paradox of Enrichment's* evolution [54].

2.4 Partial differential equations in ecology.

A considerable part of theoretical ecological research over the last few decades had addressed the fact that interactions are more than random encounters [60]. *Partial differential equations* are mainly used to model a number of ecological phenomena such as environmental invasion, dispersal of species at large [19, 58] and spatial diffusion-driven pattern formations [1, 25].

Thus, a system (3.1) model takes the same form intended to introduce *enrichment* on top of its *paradox* effects [54]. As needs be, the following question becomes a focal point: “Had various predation models in the past been built on this foundation?” [4, 57]

Conversely, for questions relating to invasion or spatial patterning, *partial differential equations* are ideal [4]. For instance, by their application to model invasion processes, it had been observed that invasion rates were always consistently proportional to those of population growth at low density and dispersal distances per generation [12, 3]. Likewise, *partial differential equations* are perfect for investigating the spatial patterning formation as they provide a mathematical tool that naturally depicts the continuous homogeneous space as a “*null model*” [28, 4].

Any patterning that develops is thus clearly due to population interplay interactions along with dispersal and not the environment itself [37]. Practical-minded ecologists might wonder why anyone would attempt to explain spatial patterning without ecological heterogeneity when all environments are so obviously incongruous [8, 26]. This is the same as asking why anyone would want to explain population fluctuations in terms of species interactions when their habitat so obviously fluctuates in time [3].

Nevertheless, much work needs to be done before *partial differential equations* realise their full potential as a tool for illuminating biological processes [4, 60]. Therefore, a

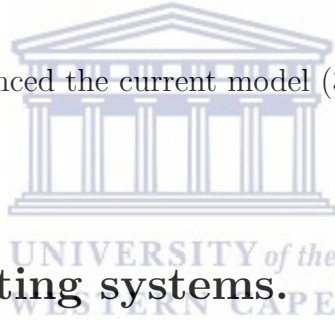
proposal has been made for the two basic primary steps to be considered:

(a) Firstly, more attention should be paid to an investigation of *transient dynamics*, how rapidly are asymptotic rates of invasion obtained and departures from simple idealised portraits of habitat shape or dispersal behavior [4].

(b) Secondly, careful comparison of many different mathematical tools available for representation is essential [40].

From mutual interactions of *Rosenzweig-MacArthur* [47], some *partial differential equation*'s interesting application results had been observed. From shared connections, once again of [47], some intriguing outcomes had been observed. In research work of *Ramanantoanina et al.* [24], a predation system had been developed through the application of *partial differential equations* with coupled ordinary differential equations. Accordingly, models (2.1-2.16) have all been built successfully using applications of *partial differential equations*.

Consequently, that has influenced the current model (3.1)'s follow-up purpose of continuing along the same trend.



2.5 Spatial interacting systems.

Original basic ecological components display spatial differences [40]. These include, amongst others, an individual species' behavior, species' abundance, diversity, and lastly species' population dynamics [22]. The spatial extent at which diseases spread and *bacteria* circulation, had been highly linked with *reaction-diffusion* models [43].

A spatial interaction is ultimately of importance in biological pattern formations [39]. Diffusion models form a reasonable basis for studying spatial interactions in *predator-prey systems* [7, 10]. Species' spatial cooperation consequently affect population dynamics [55]. Spatial interacting systems, thus provide a biological insight and are very useful in summarising, interpreting and interpolating real data [40]. Spatial heterogeneity generates spatial flows, with *local enrichment* certainly corresponding to an impoverishment elsewhere [8].

In *matlab* simulations, utilisation of spatial connections is made as they are both collectively as well as *top-down*. This support diffusion process within model (3.1) having *predator-prey interacting systems*. For future research, an alternative model can be used when a *predator-prey system* has been subjected at the highest possible level of disaggregation [22]. This will sequentially give an opportunity for the study of a *bottom-up* emergence in complex pattern formations [37]. Preferably, reflecting relationships from behavior along with interactions at an individual level [32].

It was noted in *Braverman's* [9] study that, strings of concentration rings were formed as a chemotactic pull of the bacterium *Escherichia coli* had been immunised on a semi-solid agar containing mixtures of amino acids or sugars. This was due to their response towards spatial gradients as a result of attractants produced mainly by an uptake together with catabolism [40]. Subsequently, cells drifted up the slope that had been generated synthetically by diffusion from an incline of a capillary tube or even by assimilation [8, 10]. By changing the thickness's surface, distribution of *bacteria* colonies was highly affected with greater point of moving more towards a stronger *stability* state [60, 58].

Symmetrical arrays of spots and stripes that arose consecutively were formed as *bacteria* cells developed in semi-solid agar intermediates of tri-carboxylic acid cycle [53]. More randomly, arrayed spots became visible synchronously as bacterial cells in a thin layer of liquid culture were exposed to the same compound [52].

An evidence was that in either case, patterns were stationary [29]. Excretion of chemical attractant which could be sensed by an *aspartate receptor* had been triggered by an oxidative stress [35]. An aggregation had supplied sufficient space as a mechanism of a collective defense in high cell density levels due to oxygen limitations [44]. A bacterium *Bacillus subtilis*, when immunised on a *nutrient-poor* solid agar showed evidence of fractal morphogenesis [5, 14].

For softer agar standard with a *nutrient-poor* semi-solid medium, *bacteria* colonies showed characteristics of dense morphological structures [36]. Simple circular colonies grew almost homogeneously in space as both the *nutrient* concentration and agar's softness were further increased [58]. This observation by *Murray* [40] was also relevant for

other *bacteria* types. For example, Serratia, Salmonella, Escherichia coli and their mutant strains, and references therein.

Various mathematical modeling has been developed in the past in order to explain each characteristic colony pattern [1]. These include, amongst others:

- (i) A *Diffusion predator-prey* model,
- (ii) A *Communication walker* model, and lastly
- (iii) A *Reaction-diffusion* model [10, 22].

Likewise, ecological interactions can be broadly classified as a prey-predation, competition, and mutualism [58]. However, in the work of *Li et al.* [23] and *Mcglade* [37] respectively, inter-specific interactions have been classified as a chief principal subject of ecology whereby competition as well as predation are two important factors influencing natural selection.

In *Bontje et al.*'s model [32], a *Holling type II* feeding threshold was also taken into account for *predator-prey* trophic interactions in a two dimensional system. Numerical bifurcation investigations performed with its comparative analysis given for both [32] models had identical qualitative results, but differed quantitatively. At whatever point an estimation of parameters were picked such that significant *predator-prey* dynamics of ordinary differential equations experienced sustained oscillations [54].

Equally, a *ratio-dependent asymptote* had spatially uniform oscillations with the same amplitudes [39]. This fact was also known for *ratio-dependent systems* with a *linear bifurcation term* [58]. A *proportion reliance asymptote* again had *spatially uniform* motions with the same amplitudes [3]. This reality was likewise known for proportion reliance with a *straight bifurcation term* [58].

Be that as it may, a *nonlinear bifurcation* for predators did not change the situation in [32]. According to [40], for a *prey class* (denoted by \mathbf{u}) and *predator class* (denoted by \mathbf{v}), only two possibilities for cross-terms \mathbf{f}_v and \mathbf{g}_u existed:

- (1) The main confinement had been that $f_v \cdot g_u < 0$.
- (2) In that manner, $f_v < 0$ and $g_u > 0$ or $f_v > 0$ and $g_u < 0$.

These results above must, however, correspond directly to qualitative different reactions [4]. Consequently, it has clearly been noted in *Ko-Ryu* [33]’s experimental work that reactants which promote growth in one system as an *activator* and another one being an *inhibitor*.

Quite intriguingly is that in [40], an *activator* u class also involuntary the *inhibitor*. While the inhibitor v class inhibited not only u class, but also itself [60]. For pattern formation to take place, an *inhibitor* must diffuse more quickly than its *activator* [10]. However, while in [40]’conclusion, there were fundamental changes as a v class became an *activator* which had still *self-inhibiting* and diffused more rapidly [5].

Another difference had also been noted between these two cases [39]. Patterns grew along an unstable manifold associated with a positive eigenvalue [37]. Evidence from [40]’s study was that two species were found to be at a high or low-density in the same region as patterns grew instantly. On the other hand, in cases of u class were at a high density where v class was low and contrary showed different results [40].

Qualitative features of the phase plane in vicinity of a steady state had been shown again in [40] for two cases respectively. The fact that patterns were either in or out of the phase had direct fundamental implications for biological applications [32, 31]. To get an intuitive feel for these two cases, [40] considered two different ecological *predator-prey scenarios*:

(a) In the *first case*, let u class along with v class represent the prey and predator respectively.

(i) At high a v density, u population reduced.

(ii) At low a v density, u population increased.

(iii) Also, close to a steady state, the u class had been observed to be benefiting from each other as an increase in their numbers was temporarily amplified.

(iv) Another important observation reflected that the v class decreased in numbers when a $v:u$ ratio was extremely high, but otherwise it increased.

In [40]’s comparisons above, interaction near a steady state revealed local nullclines and qualitative growth. A necessary condition for *diffusion-driven instability* in such

predator-prey situations had been that the predator dispersed faster than its prey [10, 32]. Consequently, resulting in the formation of patterns [57].

(b) Also, was to consider a *second type* of interactions in [40] with the *predator-prey* situation where *u class* presented predator and *v class* the prey respectively.

(i) In that case, the *v class* had been “auto catalytic” since when densities were too close to a steady state, there was an increase in the *u class* due to being temporarily amplified.

(ii) Increased *v class* densities improved hunting or reproductive efficiency of a *u class* [46].

(iii) Another difference between a case mentioned above and the first one is that the *u class* dispersed at a faster rate compared to its *v class* [37].

(iv) In the event wherein there was a high *u class* without diffusion, their population increased and eventually made both populations return to a steady state [10].

(v) Nevertheless, it could have happened that the *u class* grew and reduced its *v class* to a level below a steady state value [60].

(vi) In such cases, temporary increase in the *u class* was enough to prompt *auto-catalytic growth* of predators to kick in immediately [5].

(vii) Correspondingly, that resulted in a *net-flux* of the *u class* from neighboring regions which in turn caused the *v class* to drop simultaneously [46].

(viii) As *auto-catalysis* worked in the opposite direction, thereby letting the *u class* growing above a steady state value [29, 39].

These results mentioned above are of biological importance as it will be shown later their significance in *matlab* simulations.

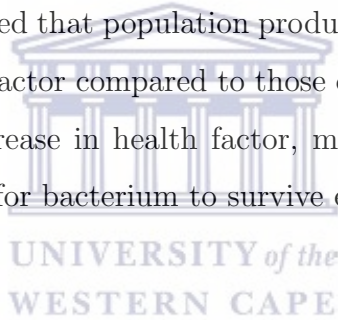
Therefore, the *instability* concept in biology is often within an ecological context, whereby a uniform steady state becomes unstable to small perturbations [57].

Properly, *predator-prey species populations* typically exhibit some temporal oscillatory behavior changes [4]. The main process driving *spatial homogeneous instability* being diffusion as a mechanism which determines spatial patterns to evolve [10, 54]. How a pattern or model is selected becomes an important aspect of research analysis as it gives

rise to the behavior of *bacteria* during diffusion processes [31]. Nevertheless, an *instability* taken as a concern of in a *spatial structured pattern* model is quite a different kind.

Quite recently, the world had been under threats with *anthrax* developments of *Krawczyk et al.* [1], as the use of biological terrorist tools emerged again. This is the same deadly catastrophic biological weapon investigated in [1] when studying a commonly deadly *bacteria* which used the application of diffusion processes with similar *matlab* simulation methods as clearly shown by *Fujikawa-Matsushita's* earlier findings [14]. The results of simulation in both [1] and [14] respectively, showed that *bacteria* colonies with rod-like structures have greatest stable fitness factors and can therefore spread out on the lattice much faster than other populations [1].

Consequently, as clearly shown in the structures of a bacterium in [1], diffusion exhibited the most dangerous infections such as those of an *anthrax*. In an *enrichment* of such systems, [1] further showed that population producing rod-like structures and spores has a smaller average health factor compared to those ones where morphing is forbidden. Thus, notwithstanding a decrease in health factor, morphing in an *anthrax* had shown that there could be a chance for bacterium to survive even in extremely hostile conditions [20].



2.6 Stability analysis, bifurcation theory and pattern formation in *predator-prey* systems.

The fundamental challenges in ecological modeling involve finding ways to deal with collective dynamics of pattern individual assembling and to scale from small to larger spatial regions [58, 44]. A central issue is an understanding of how details at one level makes its signature felt at other scales [40]. Also, how to relate transversely phenomena scales that cut across scientific disciplines along with investigating the heart of algorithmic development approaches to high-speed computation [22]. This is the case in ecology, genetics, epidemiology, and immunology [11].

An intention is made to investigate spreading of a two-dimensional bacterial population system in a surface environment. Importance of a *Lyapunov function* on *stability* includes verification and establishing local properties of such dynamical system [60, 58, 28]. This requires an auxiliary function with specific properties [9]. By comparing experimental results with numerical simulations, Braverman [9] found that *spatial homogeneous* production of *bacteria* had been an actual manifestation of growth dynamics described by *Fisher's equation*.

Therefore, analytical and numerical tools are developed for equilibrium solutions of a class of reaction-diffusion with nonlinear diffusion rates. Such equations arise from population biology and material sciences [39]. Only around the late 1990 recent research work, Rohani et al. [50] and Holmes et al. [19] obtained *global bifurcation diagrams* for various nonlinear diffusion and several growth rate functions. Diffusion mechanism illustrates a movement of many individuals in an environment or media [11]. Individuals can be very small such as basic particles in *bacteria* or very large objects such as animals [58].

Using a random analytical selection, numerical tools are employed to obtain bifurcation diagrams on equilibrium solutions of reaction diffusion models with nonlinear flow [4]. On one hand, *spatial heterogeneous* model's distribution and complex spatial patterns exhibited asynchronous dynamics which improved *stability* on *meta-population persistence* [58, 59]. Contrary, in *Li et al.*'s discovery [23], migration and predation of *predator-prey systems* with a host parasitoid *meta-population* model lead to a highly organised *spatial pattern formation*.

All bifurcation points from trivial solutions had been identified and calculated in [9]'s system (2.16). For models with a unique *non-constant equilibrium*, it was always equivalent to a critical length of its habitat [46]. Accordingly, the critical length became smaller than the one given by a bifurcation point when an Allee effect was present in such systems [46]. The Allee effect was caused by a non-monotonic intrinsic growth rate of biological species [34]. It can also happen as a result of nonlinear diffusion and monotone intrinsic growth rate [27]. It must be noted that a basic premise around *spatial structured*

patterns would be that on one hand the rate of predation would be different and also directly proportional to that of its *prey* [37].

Currently, there is still no ecological analysis of such an interaction as this *3-D spatial structured pattern*, which opens a gap for more research. Diversely, such work would be conducted and informed by the findings using a *2-D* with two similar *predator-prey* populations [19].

In other instances, as the case in [23] when oscillations of a local population had been asynchronously, *stability of predator-prey systems in meta-population* and global persistence could be highly improved [54, 58]. Otherwise, *extinction* becomes the most favorable outcome when non-linear inter-specific interactions produce strong oscillations of local populations [60].

In a follow-up study by *Mougi-Nishimura* [41], it was noted that two conditions for a *paradox* resolution are needed. Namely:

- (1) That the same prey must be preferred as a *dietary* item by both predators, creating a potential for high exploitative competition between them [54], and
- (2) While both predators are assumed to select their diet in accordance with an *optimal diet utilization* theory, one predator must be a *specialist* and another a *generalist* [22].

In a follow-up work of *Kato-Yamamura* [16], system (2.14) of equations is given by:

$$\begin{aligned}
 \frac{\partial dX_1}{\partial dt} &= \left\{ \epsilon_1 \left(1 - \frac{\partial X_1}{\partial K_1} - \alpha \frac{\partial X_2}{\partial K_1} \right) - r_1 Y \right\} X_1 \\
 \frac{\partial dX_2}{\partial dt} &= \left\{ \epsilon_2 \left(1 - \beta \frac{\partial X_1}{\partial K_2} - \frac{\partial X_2}{\partial K_2} \right) - r_2 Y \right\} X_2 \\
 \frac{\partial dY}{\partial dt} &= \{ -\epsilon_3 + K(g_1 r_1 X_1 + g_2 r_2 X_2) \} Y.
 \end{aligned} \tag{2.14}$$

Parameters of the system (2.14) are defined as follow:

ϵ_1, ϵ_2 represent the prey's growth rate,

\mathbf{K} the carrying capacity, and lastly

ϵ_3 being the predator's death rate respectively.

Also, for a resolution of the *paradox* to be met, *Mougi-Nishimura* [42] repeatedly specified two other conditions that must be contented. That is:

- (i) The same prey must be ranked higher as a dietary item by both predators creating potential for a high exploitative competition between predators [6], and lastly
- (ii) Less profitable prey must be inedible, or unpalatable and close to inedible to one *predator 2* and unpalatable close palatable to another *predator 1* [16].

The first condition (i) above was found not intuitively convincing [51]. However, it was rationally speculated that the *paradox* would not be resolved when a *two-predator-two-prey system* had different food web structures [43]. Such a system consisted a *loose coupling* of *Genkai-Yamamura* [16] and *Roseinzweig-McArthur* [47] respectively, with neither of which resolves the *paradox*.

In [16], stabilisation had been accomplished in the face of *enrichment* due to two perspectives, namely:

- (a) When an amplitude of oscillation decreased [5], and lastly
- (b) When a minimum population of all species increased (as clearly shown from *Vos et al.* [54]).

Several theoretical studies on the *Paradox of Enrichment* have focused within trophic levels for *spatial heterogeneous* models of prey types [54]. These studies showed that a difference in profitability of preys is extremely important for the *local stability* of equilibrium and the *paradox's* resolution in *one-predator-two-prey systems* [22]. This is unmistakably shown by the studies of [42, 58, 59] and reference therein.

The same was found to be true for *Kato-Yamamura's* model, which additionally showed that within trophic levels of *spatial heterogeneous* systems, a predator type is important for the *stability* of *non-equilibrium dynamics* and a *paradox's* resolution [59, 58]. Equally, in [16]'s system (2.14), their outcomes suggested that biodiversity is an important factor for ecosystem *stability* [58]. While an ecological invasion constitutes a critical role to endangered species in developing countries, for decades scientists have sought to intervene and prevent such incursions by integrating the *paradox* with *stability analysis* [19, 59].

Mathematical modeling of the *Paradox of Enrichment* in *predator-prey systems* plays a substantial role in determining which protection rate and time should be applied to

control invasion or prevent further endangerment to species [19]. In *Braverman's* study [9], a complete *linear stability analysis* of a system (2.16) of equations was presented as well as discussed [58]. Some numerical simulation results in [9] for an asymptotic behavior (with the zero Neumann boundary conditions in a 2-D domain) were similar to the relevant *Lotka-Volterra* system (2.1) of ordinary differential equations.

In a study of the *Ko-Ryu* model [33],

$$\begin{aligned}
 -\delta u &= u\left(a - u - \frac{bv}{\beta u^2 + mu + 1}\right), \\
 -\delta v &= v\left(c - v + \frac{du}{u^2 + mu + 1}\right), \\
 k_1 \frac{\partial u}{\partial v} + u &= 0, \\
 k_2 \frac{\partial v}{\partial v} &= 0
 \end{aligned} \tag{2.15}$$

had investigated sufficient and necessary conditions for coexistence states of *predator-prey interacting systems* [27]. Two species with a *non-monotonic functional response* under the *Robin boundary* conditions with $-\delta v$ in Ω and k_2 on $\partial\Omega$ had been considered.

Parameters of the system (2.15) are defined as follows:

a being the prey's intrinsic growth rate,

b as the predator's capture rate,

c as the predator's intrinsic growth rate,

d as the conversion rate of captured prey by a predator, and lastly

$\Omega \in \mathbb{R}^n$ being the bounded domain with a smooth boundary $\partial\Omega$.

In *Ko-Ryu's* view [33], a gap was discovered between two conditions, explicitly:

(1) With a *multiplicity stability* and some uniqueness of a *coexistence state* depending on some parameters reviewed [59].

(2) Due to those reasons in (1), sufficient necessary conditions for a *coexistence state* by using the *index theory* (we refer to it as ξ) were also established [58].

Furthermore, local uniqueness results of [33]'s studies with the prey (as a *nutrient*) and the predator (as *bacteria*) were significantly small. Lastly, multiplicity, uniqueness and *stability* of coexistent states were investigated under the conditions when $\beta > 0$ was

large [59]. Finally, it was shown in [33] that local existence of a coexistence state by using local bifurcation theory still uphold [58].

2.7 Matlab simulation in mathematical modeling.

A *matlab simulator* is a *spatially explicit* model frequently used in ecology to deal with local *predator-prey interactions* as well as revealing spatial structures of populations to be formed [11, 25]. A *simple grid square* had been employed to simulate *bacteria-nutrient* interactions in the SSP model. Successive states of cells arranged on a grid are calculated according to a set of rules [19]. State transitions depend both on a single cell state as well as in the local neighborhood [40]. Having the ability to generate large scale pattern formations from diffusion, local interaction application in *matlab* simulation is quite of relevance and a reliability.

In the study of spatiotemporal dynamics, *Zhang et al.* [25] described the most significant acceptable approach use of *numerical simulation* along with *ratio dependence* systems. Utilisation of a *spatial pattern* simulation had been applied in details by *Krawczyk et al.* [1], reflecting numerical analysis of a *bacteria* population. What is quite relevant in [1]’s study is that a two dimensional *numerical simulator* had been used similarly to the one being examined in *SSP* model’s study.

Certain assumptions in [1] had been made into *bacteria* modeling as it had been treated as an independent agent. That is, being able to interact with its surrounding environment while it can exponentially grow under certain sets of rules [25]. Competition in an investigative work of *Colasanti et al.* [11] showed exclusion of *annuals* by *perennials* due to recruitment happening inside the matrix empty cells.

Amalgamation models of *Colasanti et al.* [11], also found that it is still possible to create a new model which has a potential to capture some of the consequences for both competitive and ruderal traits. A note of significance was that competition had been associated with low stress and low disturbance, while the ruderal traits with low stress and high disturbance [4]. The product for a fully assembled physiological description of

a *plant-functional system* had been accomplished with an addition of a tissue longevity together with lifespan traits that survived in the absence of any resource allocations [11].

Hence, that lead to [11]’s results, which explained the behavior inside the *matrix protocols*, whereby environment had been described at a level of an individual cell from within. Each cell observed displayed a disconnected assessment probability of access to resources and the plant in such a cell being destroyed. In the recent study of *Molchanov* [38], a focus had been based upon an incorporation of three *stochastic* models for fractal growth to a single form. The newly formed model by [38] after incorporation of the three independent ones presented a realistic trade-off.

However, [38]’s investigation represented a theory of diffusion process which clearly defined transition of a growing pixel cluster into *Laplace equation*. That took into consideration two families of operators which were generated by a *Markov’s* process [37]. Observations undertaken into [38] clearly defined a basic assumption for the formation of patterns, while conversely, it represented a good understanding of the *thickness effect*.

All models mentioned above have some basic rules of operations, which had been clearly defined ecologically in details by [38] within the context of *enrichment*. In order to achieve that, initial stages required substitution of the *Brownian motion* with a universal stochastic process compromising jumps and long range dependency flights [38]. It had been noted that directions of flight as an isotropic still influence the cluster’s thickness [3]. An application of a map lattices as a strong point for constructing foundation in a number of predation models in the past had been applied [40].

In [25]’s study, a closer look had been taken to evaluate the role of distribution patterns in *meta-population* models. Two different models had been used, namely, a *Levins’s meta-population* model and *Probability transition* model respectively [25]. Focus closely was then on a community of three species in cyclic competition [54]. Quite excitingly is the *Levins’s* model which at some point resembles that of *Braverman* (the model under review.)

In [9] of *Braverman* model, a system of equations is given by

$$\begin{aligned}\frac{\partial n}{\partial t} &= \nabla^2 n - \frac{nb}{1 + \gamma n} + rn\left(1 - \frac{n}{M}\right), \\ \frac{\partial b}{\partial t} &= \nabla(\sigma nb \nabla b) + \frac{nb}{1 + \gamma n} - \beta b.\end{aligned}\tag{2.16}$$

Parameters of the system (2.16) are defined in detail in [9] (and reference therein).

Remark 2.7.1. *The index of Enrichment formulation.*

Definition 2.7.2. Let the *index of enrichment* (we refer to it as $\xi(M)$) be a sum of an energy value ξ as well as the carrying capacity M defined by $\xi(M) = \xi_0 \eta$ for all $M \geq M_c$. Then $\xi(M) = \frac{\xi_0}{1 + \beta(M_c - M)}$ as $M < M_c$ with β being the measurement of a declining energy value in response to unit levels of an inclined carrying capacity beyond some critical value M_c .

A realistic behavior of community response to an *enrichment* in which *stability* of dynamics is sustained would be depicted by a suitable $\xi(M)$ [4]. Lastly, to include a prey's caloric content in description of *enrichment*, two real parameters are introduced, namely, a ϵ and η such that $\epsilon = \xi\eta$.

Hence, [25] showed the effects of colonization rates based on *Levins's* model for three non-interacting species along with distribution of dynamical behavior in *predator-prey systems*. *Levins's spatially implicit assembly* occurred within the mean field assumption foundation with a potential during simulations to display three different effects, specifically:

- (i) Dynamics of damped oscillations,
- (ii) Periodical fluctuations, and lastly
- (iii) Stage-equilibrium.

Construction of a *Probability transition* model as a spatially explicit display was simply based on *Markov's process* [40]. On both [25]'s models above, a random dispersal was allowed as well as diverse distance in *spatial homogeneous* patchy

environments which demonstrated the loss of *stability* as a *dispersal distance increase's* result [60]. In addition to this factor, [25] also established that species diversity highly dependent upon two factors, namely, a *local distance* and *interactions* respectively [19].

Effects of *enrichment* amongst interacting species had been clearly shown in [25] using a *Tilman's multi-species* model with intended results leading to the *Paradox of Enrichment*. Conversely, a *long distance dispersal* might lead to species *extinction* [19, 54]. Currently, there are only two ways of dealing with the dispersal of organisms in mathematical models, that is, a *local* and *global dispersal* respectively [22].

Recent studies toward spatial *predator-prey* models have revealed that limited dispersal of organisms with a temporal, *spatial heterogeneous* environment encourages *stability* as well as *persistence* [58, 59]. The results from *Courbau et al.* [7] have shown that the more there is an increase in colonisation rates for a given species, it contradictory decrease its own *global occupancy*. Equally so, promoting that of its superior competitor [29].

A *Probability transition* model took into consideration the lattice display based on simulations in the study of spatial dynamics and formation of patterns [12]. All patches in two-dimensional lattice were orderly arranged with integer coordinates [25]. Taking into consideration both the *von Neumann* and *Moore neighborhood*, respectively, migrants to a patch arose from within neighboring patches surrounded by its dispersal kernel [19].

Outstanding challenges as a result of environmental devastation and fragmentation throughout the world had given *meta-population* model a space within which it could be used as an essential tool for conducting research based concepts targeting conservation biology of spatial ecology [52]. A simple competitive hierarchy had classified species into ranks ranging from the best *competitor* to the *poorest* [53]. Therefore, there would be traces of open patches to accommodate *stable coexistence* basis within competitive species [3].

Direct interactions amongst species and *paradoxical diversity* responses in complex interlinked communities can affect both an existing and population growth of a given species [19]. As it is true that evolution favors most competitive individuals within a

given species, on the contrary, it leads to a species population decline. A *voter system* with three species had shown similar contradictions [13]. All these paradoxes above, are very comparable to [25]’s *Levins* model.

2.8 Main conclusions reached from above model studies.

In this section, highlights are being given for models (2.1-2.16) that have been studied towards the *Paradox of Enrichment* as far back as its evolution. Notwithstanding, despite the fact that there are steps of advancements, all these models share some basic fascinating findings which incorporate the accompanying:

- (i) The role of *enrichment* in interacting *predator-prey systems*,
- (ii) Use of *partial differential equations* in ecology at large,
- (iii) Spatial pattern formation using *reaction-diffusion driven systems* in *spatial heterogeneous* models [26], and lastly
- (iv) The role of oscillations under *unstable* conditions.

A summary of the current investigate findings with regard to the *Paradox of Enrichment* is also reflected in Table (2.1).

Technical and substantive concerns were raised in *Lotka-Volterra’s* model [47] based on system (2.1) which undermined its empirical usefulness. To mention a few:

- (a) Practical, realistic concerns occurred in [47] as each closed orbit became only weaker along a steadiness “borderline” between *stability* and *instability*.
- (b) As a result, in (a) above, following a small shock, [47]’s system (2.1) neither returned to its *original equilibrium* nor continued to diverge from it.
- (c) To a certain extent, the system (2.1) simply “collided with itself” onto a new closed orbit where it remained indefinitely (unless hit by a subsequent shock).
- (d) From [47]’s phase diagram, it was also noticed that trajectories spiraled around an interior steady state.

(e) Again, it became unclear graphically whether trajectories spiraled inward (*stability*) or outward (*instability*).

To be more specific, starting from any initial condition in [47], trajectory eventually returned to a cyclic point and the system (2.1) of equations continued along a “closed orbit” forever. That result in [47] never holds for *discrete-time* version models where orbits are not closed but instead spiral outward.

Hence, [47]’s system (2.1) of equations exhibited weak *stability*. However, in models with a continuum of *weakly stable equilibria*, small specifications of dynamics can have large qualitative effects. These, in turn, can dramatically alter a number and *stability* of equilibria. In the parlance of dynamical systems, such models are not structurally stable. This called into question the robustness of any predictions derived from systems (2.1) of equations. Incidentally, spirals had been observed in [47] as not a unique feature of all realistic population interactions.

Rosenzweig-MacArthur’s system (2.2) of equations included a *density-dependent prey growth* with a *functional response* [47]. However, the model assumed fixed *predator-prey interaction* links which were not realistic in nature. For this reason, *Roy-Chattopadhyay* concluded that [47]’s outcomes were then limited only in the direction of both laboratory and experimental observations respectively [51]. Enriching ecosystem’s *nutrient* energy flow in most arising world’s demand had strong devastation end results [48, 49]. Application of multiple realistic models in *nutritional enrichment* of two-species interactions resulted towards *instability* [40, 19].

In a system (2.3) of equations, *Rosenzweig* [48] noticed that oscillations in *predator-prey ecosystems* would not last forever, hence limiting formation of spatial patterns. Not all *equilibrium points* resulted in a steady state due to its position to the *prey’s isocline* (also referred to as a *hump*). A *critical value* of *equilibrium point*, say V^* thus defined the *humps* peak. Although [48]’s model had been well accepted as a classic example of ecological theory, the word “*paradox*” in its phrase had not yet been universally acknowledged [51]. Accordingly, *Mougi-Nishimura* [41] recognised that it had been subjected to different interpretations [31].

However, in subsequent articles, the phrasing “*paradox*” had been used to express discrepancy between dynamic behavior of real simple *predator-prey systems* [12, 5, 32]. While *Rosenzweig’s paradox* work had been highly accepted on one side, [41] challenged the extrapolation of [48]’s theoretical analysis and its universality in more complicated mathematical interacting realistic systems [54].

To discover the *Paradox of Enrichment*, [48] concluded that in the effects of enriching a system, one needs to find how an *equilibrium point* V^* changes as *enrichment* proceeds and also take note on the relationship between V^* and \mathbf{V} population. In addition, $V^* = J$ (*predator’s isocline*) meant that the system was in a steady state. If an *enrichment* increases V^* , then it is jeopardizing the system, because eventually V^* will be made greater than \mathbf{J} .

Treating species’ population as molecules in [48] had been shown to be inadequate. Consequently, *Roy-Chattopadhyay* [51] argued that there was a lack of scientific natural convincingly results in all six models tested. Once more, *enrichment* unambiguously tends to weaken steady state [16]. *Jensen-Ginzburg* [30] reflected that conclusion based on [48]’s outcomes did not apply to natural ecosystems, as a result limiting parameters of setting *enrichment* in reality.

Limitations existed in *Tilman’s* model (2.4) [53] on the basis that competition interactions were negatively summarised in the effect of each species on a growth of all others. *Hirsch* [22] outlined that there was no explicit statement on the causes of such negative effects. Competition models therefore provided no guidance as they became more descriptive than predictive [51]. The use of measures in resource utilization overlapped to approximate parameters of *Lotka-Volterra’s* equations as it lacked a theoretical basis for making such untrue estimations [37].

Formulation of competition models that explicitly state mechanisms for a contest amongst interacting species is needed [39]. Consequently, [53]’s model served as not a complete, exhaustive treatment of resource based approaches to population and community ecology. Hence, [53] concluded that limitations of mathematics in the main text to algebra and graphic techniques were not assured in real world interaction systems.

In *Pimms's* work [46], research methodology had been limited to integrating food webs with the rest of ecological theory. An obvious next step was to connect food web structures and body sizes with species abundances [43]. However, *Genkai-Yamamura* [16] concluded that [46]'s work left a huge gap in the field of *ecological stable ecosystems*.

Consequently, an alternative prey made it possible in *Holt-Polis* [20] for a shared prey species to be excluded, in which case formal conditions never hold involving *intraguild predation*. With both linear and nonlinear models, there had been a strong variety of impacts upon such *stability* [9].

Moreover, an accumulation of weak interactions stabilised system (2.6), whereas adding relatively strong interactions had a destabilising tendency in terms of both population fluctuations and coexistence respectively [7]. In both linear *Lotka-Volterra systems* and nonlinear *intraguild predation* models, with or without an alternative prey, given cycles or chaotic dynamics, densities often reached very low values where stochastic demographics had likely nudge species toward *local extinctions* [44]. Subsequently, [20] suggested that an important direction for future work in general would be to embed analysis of community systems into richer webs of interacting species across *spatial heterogeneous* models and patchy landscapes.

An alternative *ratio dependent structure* in *Arditi-Ginzburg* [2] provided many predictions that seem more reasonable. Such forms had also been directly supported by many empirical observations, including the likes of [44]. Consequently, system (2.7) described an *extinction* in the model by complete prey exhaustion with limitations as being unable to generate such outcomes. In both [2]'s models, limit cycles arose when *conversion efficiency* exceeded a certain critical value.

It is based on these reasons mentioned above that [2] suggested a *traditional prey-dependent form* would apply to simple *spatial homogeneous systems* with rapid turnovers. Those forms appeared more comparable to chemostats with predation essentially a continuous local process. A *ratio dependent system* seemed more appropriate in a complex *spatial heterogeneous* environment where the final large-scale outcome of predation was a sharing process [55].

Along those lines, [2] anticipated that future work should investigate more closely how behavioral and physiological mechanisms must be translated to a large scale of population dynamics. Optimistically, that accumulation of evidence will allow clear delineation areas of applicability for two opposite idealisations [42]. Namely:

(1) Other models incorporating an assumption that the predator's attack rate depended upon a (*predator:prey*) ratio abundances [5].

(2) Henceforth, claiming that *enrichment* not predicted to be destabilising [2].

Spatial heterogeneous models in Arditi et al. [3] had not been given priority as it only appeared spontaneously as a result of reaction-diffusion to a predator acceleration's response. Correspondingly, pure diffusive models and *conventional* models previously failed to demonstrate heterogeneous regimes on a short time scale [8]. Thus, taking into account local interactions and boundary conditions using systems (2.10) of equations [13].

Experimental work on *Pieluo* [45]'s display (2.9) had shown that logistic equations have been never realistic for a food-limited population under the effects of environmental intoxicants. Hence, [45] established a new growth function thereafter with the dynamics of a population where growth limitations had been based on the proportion of available resources not utilised [40]. Be that as it may, [45] concluded that pattern formations in the case of *Holling Type II predator-prey* models with a *ratio dependent-functional response* still remain an interesting area of research in ecology?

According to *Bazykin et al.* [5], multiple *stability* states coexisted amongst *predator-prey dynamics*, resulting in a complete *extinction* of both species. However, [45]'s model (2.9) lacked support on an impact of structural sensitivity due to a number of stable states [28]. Based on this regard that [5] raised two important questions of interest along his findings:

(i) How many complex ecological systems could be affected by sensitivity to a model formulation?

(ii) How to deal with such uncertainties in model predictions?

This brought about a challenging way of research as [5] was concerned. That is:

(a) For a better assessment of model uncertainties, and lastly

(b) Accurate model predictions.

The *Paradox of Enrichment* occurred in *Haque's* [18] system (2.11) of equations for certain parameter values while the “*functional response*” was of a *ratio dependent*. A *Turing instability* arose for [18]’s modified model as well as [5]’s original model with *prey-dependent* “*functional response*” (reference in of Appendix B of [18] in a certain parametric space).

Unthinkingly, [18] concluded that the difference linking *prey-dependent* with a *ratio-dependent predator-prey* model was no longer valid when the predator’s competition had been accounted for. Finally, [18] accomplished that competition within the predator population might be of beneficial for predator species under certain circumstances in a deterministic environment [40].

Beddington-DeAngelis [6]’s system (2.12) of equations very similar to the well-known *Holling Type II* model with an extra term “*by*” in the denominator which modeled a mutual interference among predators [6]. System (2.12) had some of the same qualitative behaviors as the *classical ratio-dependent* model, but is free from singular behaviors at low densities, making such point a source of controversy.

A salient statistical evidence from nineteen *predator-prey systems* proved that the [6]’s “*functional response*” model provided a better description of predators feeding over a range of resource abundances. While in some cases, system (2.12) of equations performed better than other general “*functional response*” models.

According to [6], all early *predator-prey* models demanded that a defined “*searching efficient equilibrium*” should be constant. An assumption had been shown in the application of system (2.12) of equations to be wrong in two ways, namely:

(i) With the first indication that efficiency declined as the prey density increased, and lastly

(ii) That an equilibrium declined with increasing predator density.

In follow up developments, *Genkai-Yamamura* [16] showed that the *Paradox of Enrichment* never occurred in experimental and natural communities. Using system (2.14) of equations, [16] presented a theoretical model that describes a novel mechanism

for resolving the *paradox* in cases of a predator with an *optimal selective feeding*.

According to [16], sufficient *enrichment* of the prey led to a destruction risk of *predator-prey system*. Three noticeable findings from [16] had been that:

- (i) Such *enrichment* firstly destabilised a *stable equilibrium point*, resulting in a limit cycle.
- (ii) Amplitudes of population oscillations grew rapidly, and lastly
- (iii) While the minimum population abundances approached zero, *enrichment* further increased, resulting in stochastic effects leading to *extinction*.

In spite of astonishing predictions for *classic* models, the *paradox* had seldom been tested empirically. *Ratio-dependent displays*, however, were found to be less widely accepted than *prey-dependent* models with an attack rate depended on an instantaneous prey density [30]. Equally, none of these studies considered cases in which equilibrium was unstable and the system followed a limit cycle [54].

In *Beddington-DeAngelis's extension* model (2.13) applied by [16], the *Paradox of Enrichment* had been reviewed to be different from other previous ones. This was based on the conditions that switching predators that dealt with non-equilibrium dynamics of limit cycles displaying optimal selective feeding strategy [4]. Consequently, that maximised energy input highly dependent on the profitability as well as its prey abundances [16]

Therefore, if *enrichment* increased only intrinsic growth rate, the *paradox* problem would not exist in the first place [39]. This reason mentioned above enforced [16] to confine his study to the *carrying capacity* effects on *predator-prey dynamics*.

Also taking into consideration that most real communities are more complex than ones analysed under system (2.12) of equations [29]. Even though reviewed studies before noticed difficulties in analysing communities incorporating species with more realistic links, [16] suggested that it was an important and open problem to be solved systematically.

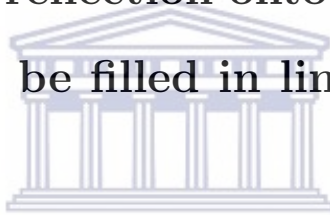
In view of *Ko-Ryu* [33], a gap was discovered between two conditions in which *multiplicity, stability* and some uniqueness of *coexistent* states depending on set

parameters had been reviewed, namely:

- (i) Due to some sufficient necessary conditions for an existence of coexistent states by using ξ theory were also established [7].
- (ii) *Multiplicity, uniqueness and stability of coexistent states* were investigated, under the conditions when β was large [26].

Finally, it was also shown in [33] that local existence using a *bifurcation theory* still uphold. *Braverman* [9] used *spatial homogeneous system* to test effects of *enrichment*. Hence, systems (2.16) of equations had a high potential of being used for *computer environmental* simulations when reviewed under *spatial heterogeneous* models.

2.9 An overview reflection onto knowledge gaps that still needs to be filled in line with the *Paradox of Enrichment*.



A major gap challenge noted by *Roy-Chattopadhyay's* study of mathematical modeling in ecology had been highlighted to still exist [51]. This includes amongst others:

- (i) That in ecological research there is still a huge gap which needs to be filled by the current and future planned studies [22].
- (ii) There is a serious need to do more research work which fits well with real natural challenges that the world is faced with [40].

The main focus here is to give an overall review of both empirical and theoretical works that are directly related to the *Paradox of Enrichment*. Therefore, the work will be divided into three categories, namely:

- (a) Experiments and field observations on the *paradox* together with some fundamental theories proposed to resolve it [54].
- (b) The handful use of experiments cited by a number of authors which claimed that *enrichment* causes destabilisation of ecosystems [28].

Model	Author and year	<i>Paradox of Enrichment</i>	Conditions
2.1	Lotka-Volterra 1925	Happens	Conditional,
2.2	Rosenzweig-MacArthur 1963	Happens	unconditional
2.3	Rosenzweig 1971	Happens	unconditional
2.4	Tilman 1980	Happens	unchanged
2.5	Pimm-Lawton 1978	Happens	unconditional
2.6	Holt-Polis 1997	Happens	Unconditional
2.7	Arditi-Ginzburg 1989	Happens	Unconditional
2.8	Arditi-Ginzburg 1989	Does not happen	
2.9	Pielou 1969	Happens	Unconditional
2.10	Bazykin 1998	Happens	Conditional
2.11	Haque 2009	Happens	Conditional
2.12	Beddington-Deangelis 1975	Happens	Conditional, when $a \leq eb$
2.12			and $emc \geq ahy(ax + by + c)$
2.13	Beddington-DeAngelis 1975	Happens	Conditional if $a \leq eb$
2.14	Kato-Yamamura 2000	Happens	Conditional
2.15	Ko-Ryu 2006	Happens	Unconditional
2.16	Braverman 2007	Happens	Conditional

Table 2.1: Conditions for the “*Paradox of Enrichment*” of the models (2.1-2.16).

(c) There is a strong argument that the *Paradox of Enrichment* does exist. In other research studies reviewed, a major challenge was whether it is reversible [6].

2.10 How will analysis be conducted using the chosen model?

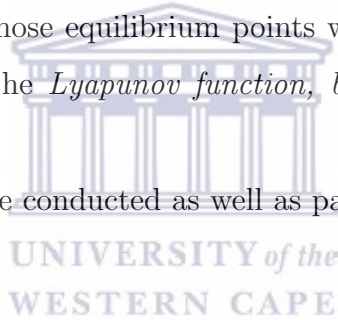
The first important step would be to look into *Braverman's* system (2.16) and see how can it be improved [9].

That would require a small disturbance and different technique tools to test *stability analysis* of each equilibrium point [19, 27].

Then, the parameters of a newly transformed *Spatial Structured Pattern* model needs to be adjusted in order to fit numerical simulations and establish each state of equilibria [13].

The utilisation of *Neumann's boundary conditions* where an explicit finite different scheme in the second order of the coordinates is applied in system (3.1) simulations [58]. *Stability analysis* of each of those equilibrium points would be conducted using suitable mathematical tools such as the *Lyapunov function, bifurcation analysis, diffusion* and *Brownian motion* [28].

Finally, *matlab* simulations are conducted as well as parameter estimations.



Chapter 3

The Spatial Structured Pattern model.

The main purpose of this chapter is to introduce the *spatial structured pattern* model, which is a modification of the model in [9] of Braverman and [17] of Goodnight et al. This *SSP* model forms the basis of our investigation, and in particular the computational investigation using *matlab simulator*. Three equilibrium points are studied very similar to those of Bohannan [8] along with *stability analysis* in *SSP* models. We subject [9] to *enrichment* as explained under Remark (2.7.1).

3.1 Representing the System.

The *spatially structured pattern* model that forms the basis of our study of the paradox of enrichment is as below:

$$\begin{aligned}\frac{\partial n(x, y, t)}{\partial t} &= \nabla^2 n - \alpha g_n \frac{nb}{1 + \gamma n} + n f_n \left(1 - \frac{n}{M}\right), \\ \frac{\partial b(x, y, t)}{\partial t} &= \nabla(\sigma n b \nabla b) + \beta g_n \frac{nb}{1 + \gamma n} - \theta b,\end{aligned}$$

for suitable functions $f(n)$ and $g(n)$ which we write as g_n and f_n respectively. We assume that $g(n)$ and $f(n)$ are monotone with continuous non-zero first order derivatives.

Parameters of System (3.1) are then as follows.

ϵ is the product of the predator conversion factor η along with the prey's biomass energy value ξ .

$n(t, x, y)$ is the *nutrient* concentration at point (x, y) ,

$b(t, x, y)$ is the bacterial cell's density at point (x, y) ,

M is the carrying capacity of the lattice environment for the nutrient,

α is the *nutrient's* diffusion coefficient,

σ is a *bacteria's* diffusion coefficient,

f_n is a *nutrient's* population growth function in the absence of *bacteria* (predator),

θ is a *bacteria's* population decline function in the absence of its *nutrient* (prey),

α , β and γ are the parameters of the Holling Type II functional response,

g_n is the functional response that defines how rates of predation differ with that of prey density.



This system has the following equilibrium points:

A zero equilibrium Q_0 with $n = b = 0$,

A bacteria-free equilibrium Q_1 with $n = M$ and $b = 0$, and also

A co-existence equilibrium Q_2 .

In the case of g_n being a constant function $g_n = g_0$, then for Q_2 we have the coordinates:

$$n = \frac{\theta}{\beta g_0 - \gamma \theta} \text{ and}$$

$$b = \frac{f_n}{\alpha g_0} \left(1 - \frac{\theta}{M(\beta g_0 - \gamma \theta)}\right) \left(1 + \frac{\gamma \theta}{\beta g_0 - \gamma \theta}\right).$$

In the more general cases, coordinates of the point Q_2 cannot be expressed so explicitly, and one may have to resort to numerical solutions.

We now proceed to calculation of the Jacobian matrix which determines local stability of the endemic points. Firstly, we write

$$\begin{aligned} F_1 &= \nabla^2 n - \alpha g_n \frac{nb}{1 + \gamma n} + n f_n \left(1 - \frac{n}{M}\right), \\ F_2 &= \nabla(\sigma n b \nabla b) + \beta g_n \frac{nb}{1 + \gamma n} - \theta b. \end{aligned}$$

Given any non-negative value n_0 , we consider a small perturbation on n_0 and we express the perturbed value in the following form, with λ being a growth rate, w_1 and w_2 being wave numbers and ϵ very small:

So we consider:

$$n = n_0 \exp[\epsilon(\lambda t(w_1 x + w_2 y))].$$

Then

$$\nabla^2 n = \epsilon i^2 n (w_1^2 + w_2^2) = -\epsilon n (w_1^2 + w_2^2),$$

In particular then,

$$\frac{\partial(\nabla^2 n)}{\partial n} \Big|_{Q_0} = 0 = \frac{\partial(\nabla^2 n)}{\partial n} \Big|_{Q_1} = \frac{\partial(\nabla^2 n)}{\partial b} \Big|_{Q_0} = \frac{\partial(\nabla^2 n)}{\partial b} \Big|_{Q_1}.$$

We can express b in a similar form as we did for n above. We then calculate $\nabla(\sigma nb \nabla b)$ and find that

$$\left[\frac{\partial}{\partial n} \nabla(\sigma nb \nabla b)\right]_{Q_0} = 0 = \left[\frac{\partial}{\partial n} \nabla(\sigma nb \nabla b)\right]_{Q_1},$$

and

$$\left[\frac{\partial}{\partial b} \nabla(\sigma nb \nabla b)\right]_{Q_0} = 0 = \left[\frac{\partial}{\partial b} \nabla(\sigma nb \nabla b)\right]_{Q_1}.$$

The Jacobian matrix $J(Q)$ at a point Q takes the form

$$J(Q) = \begin{pmatrix} \frac{\partial F_1(Q)}{\partial n} & \frac{\partial F_1(Q)}{\partial b} \\ \frac{\partial F_2(Q)}{\partial n} & \frac{\partial F_2(Q)}{\partial b} \end{pmatrix}.$$

We can now calculate these partial derivatives at the two equilibrium points Q_1 and Q_2 .

Firstly, we note that:

$$\frac{\partial F_1}{\partial n} = -\epsilon n(w_1^2 + w_2^2) - \alpha g'_n \frac{nb}{1 + \gamma n} - \alpha g_n \frac{b}{(1 + \gamma n)^2} + f'_n \left(n - \frac{n^2}{M}\right) + f_n \left(1 - \frac{2n}{M}\right).$$

and

$$\frac{\partial F_1}{\partial b} = \alpha g_n \frac{n}{1 + \gamma n}.$$

Therefore we obtain

$$\left.\frac{\partial F_1}{\partial n}\right|_{Q_0} = [-\epsilon(w_1^2 + w_2^2) + f_0]_{Q_0} = f_0,$$

and

$$\left.\frac{\partial F_1}{\partial b}\right|_{Q_0} = 0,$$

$$\left.\frac{\partial F_1}{\partial n}\right|_{Q_1} = -f_M,$$

$$\left.\frac{\partial F_1}{\partial b}\right|_{Q_1} = \alpha g_M \frac{M}{1 + \gamma M}.$$

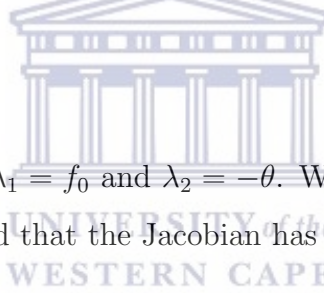
We also calculate

$$\frac{\partial F_2}{\partial n}|_{Q_0} = \left[-\beta g'_n \frac{nb}{1 + \gamma n} + \beta g_n \frac{n}{(1 + \gamma)^2} \right]_{Q_0} = 0,$$

$$\frac{\partial F_2}{\partial n}|_{Q_1} = 0,$$

$$\frac{\partial F_2}{\partial b}|_{Q_0} = \left[\beta g_n \frac{n}{1 + \gamma n} - \theta \right]_{Q_0} = -\theta,$$

$$\frac{\partial F_2}{\partial b}|_{Q_1} = \beta g_M \frac{M}{1 + \gamma M} - \theta.$$



Thus at Q_0 , the eigenvalues are $\lambda_1 = f_0$ and $\lambda_2 = -\theta$. With $f_0 > 0$, it follows that Q_0 is unstable. At the point Q_1 we find that the Jacobian has the eigenvalues:

$$\lambda_1 = -f_M \text{ and } \lambda_2 = \beta g_M \frac{M}{1 + \gamma M} - \theta.$$

Consequently, we have proved the following theorem

Theorem 3.1.1. :

- (a) The zero equilibrium Q_0 is unstable.
- (b) The bacteria-free equilibrium Q_1 is locally stable if $\theta > \beta g_M \frac{M}{1 + \gamma M}$. Otherwise Q_1 is unstable.

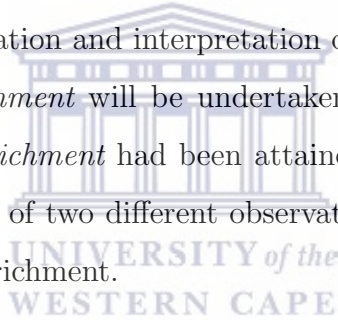
Let us now turn to endemic equilibria. We note that in the paper [9] of Braverman and [17] of Goodnight et al, in which the model is a special case of the model above, the stability study of the equilibrium point Q_2 becomes extremely complicated. Eventually in Bravermans' paper the problem is restricted to certain specific numerical values of the parameters and the stability is explained only for this special scenario. We certainly do not attempt here to analytically solve this problem. It is best left to numerical investigation.



Chapter 4

Numerical simulations and the results.

In this chapter, a closer consideration and interpretation of two prominent models in addressing the *paradox of enrichment* will be undertaken. In the [56] of *Weide et al.* model, a positive *paradox of enrichment* had been attained, while in the [41] of *Mougi-Nishimura* model, a combination of two different observations had been achieved in line with resolving the paradox of enrichment.



4.1 Numerical simulations.

The main purpose of this section is to carry out some simulation runs for different values of M using the matlab programme. An observation in to the dynamic behavioral change of the SSP model would be highly significant. Consequently, a detailed analysis will be given highlighting the noticeable reactions of the SSP model subject to parametric changes.

The model in [56] had been established by an extension of the *Nicholson-Bailey* model [52]. The transformed [56] had an inclusion of a logistic prey growth with a type II functional response. N_t and P_t denotes the population densities of the prey and the predator respectively over time ranging from t to $t + 1$. It takes into account diverse

sequences of events in the period ($t \rightarrow t + 1$).

In consideration of the order of events, the prey per capita growth and the introduction of dimensionless variables, a non dimensional predator-prey model of [56] is then represented by

$$\begin{aligned} N_{t+1} &= N_t F(N_t) \cdot e^{\left(\frac{-P_t}{1+N_t F N_t}\right)}, \\ P_{t+1} &= b N_t F(N_t) \left[1 - e^{\left(\frac{-P_t}{1+N_t F N_t}\right)} \right]. \end{aligned}$$

The parameters of *Weide's* model are defined in detail in [56] and references therein.

Let X_i ($i = 1, 2$) and Y_j ($j = 1, 2$) represent the densities of the prey and predator in a two-predator-two-prey system. The model in [41] is thus represented by

$$\begin{aligned} \dot{X}_i &= \left\{ r_i \left(1 - \frac{1}{K_i} \sum_{k \in \text{preytypes}} \gamma_{ik} X_k \right) - \sum_{j \in \text{predator types}} \mu_{ji} Y_j \right\} X_i, \\ \dot{Y}_j &= \left(b_j \sum_{k \in \text{preytypes}} g_{ji} \mu_{ji} X_k - d_j \right) Y_j, \end{aligned}$$

with the value of μ being given by

$$\mu = \frac{p_{ji} \epsilon_{ji}}{1 + \sum_{i \in \text{preys}} p_{ji} h_{ji} \epsilon_{ji} X_i}.$$

The parameters of *Mougi-Nishimura's* model are defined in detail in [41] and references therein.

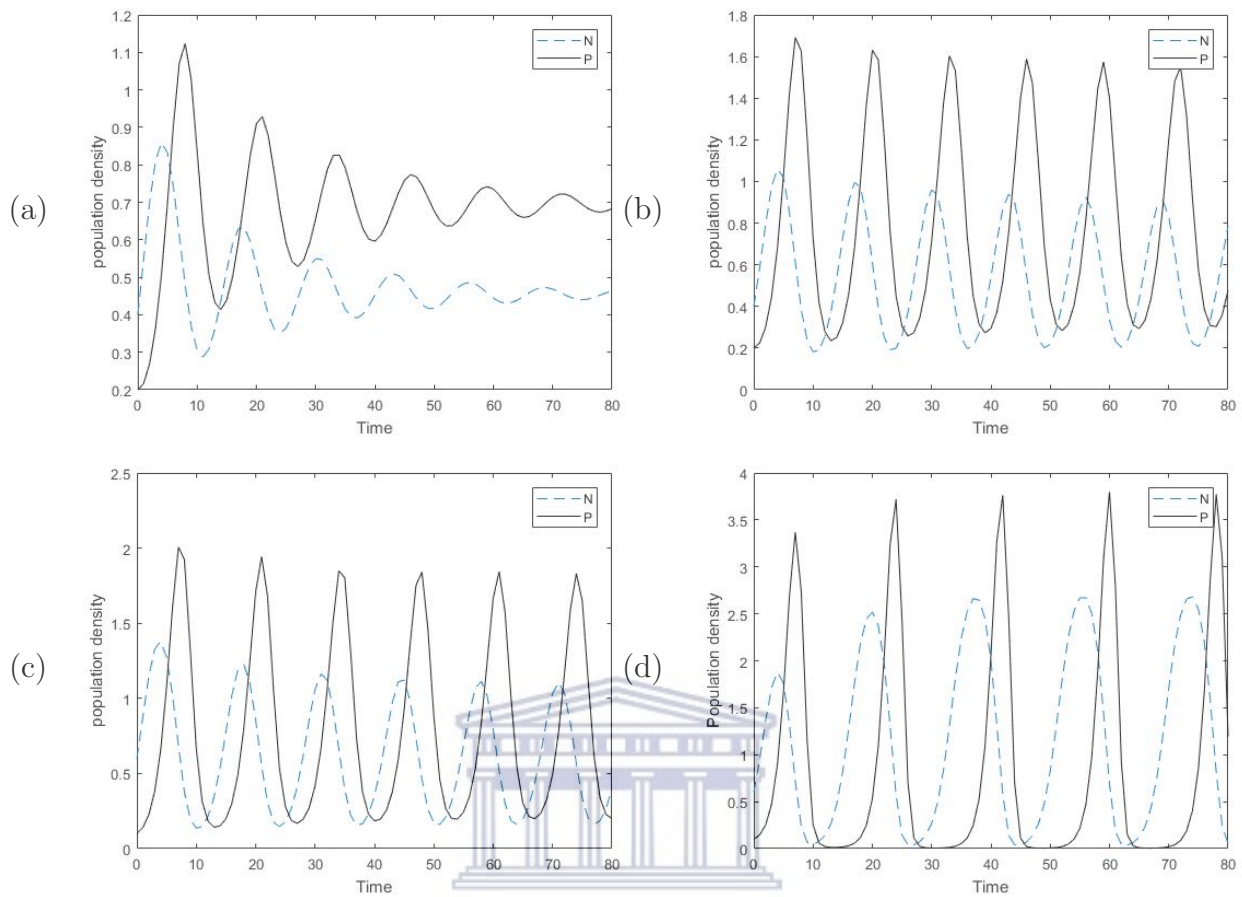


Figure 4.1: Underlying mechanisms that generate system stabilization with increasing enrichment. The solid black line represent the bacteria's density. The dotted blue line represents the nutrient's density. **Initial conditions** and parametric values are set as follows: (a) $r = 3$, $M = 1.45$, $\gamma = 0.1$, $\beta = 5$, $\delta = 2$, $\sigma = 2 = \lambda$, $N(1) = 0.4 = n$ and $P(1) = 0.2 = b$. In (b), (c) and (d) only M changes while other parameters stay the same.

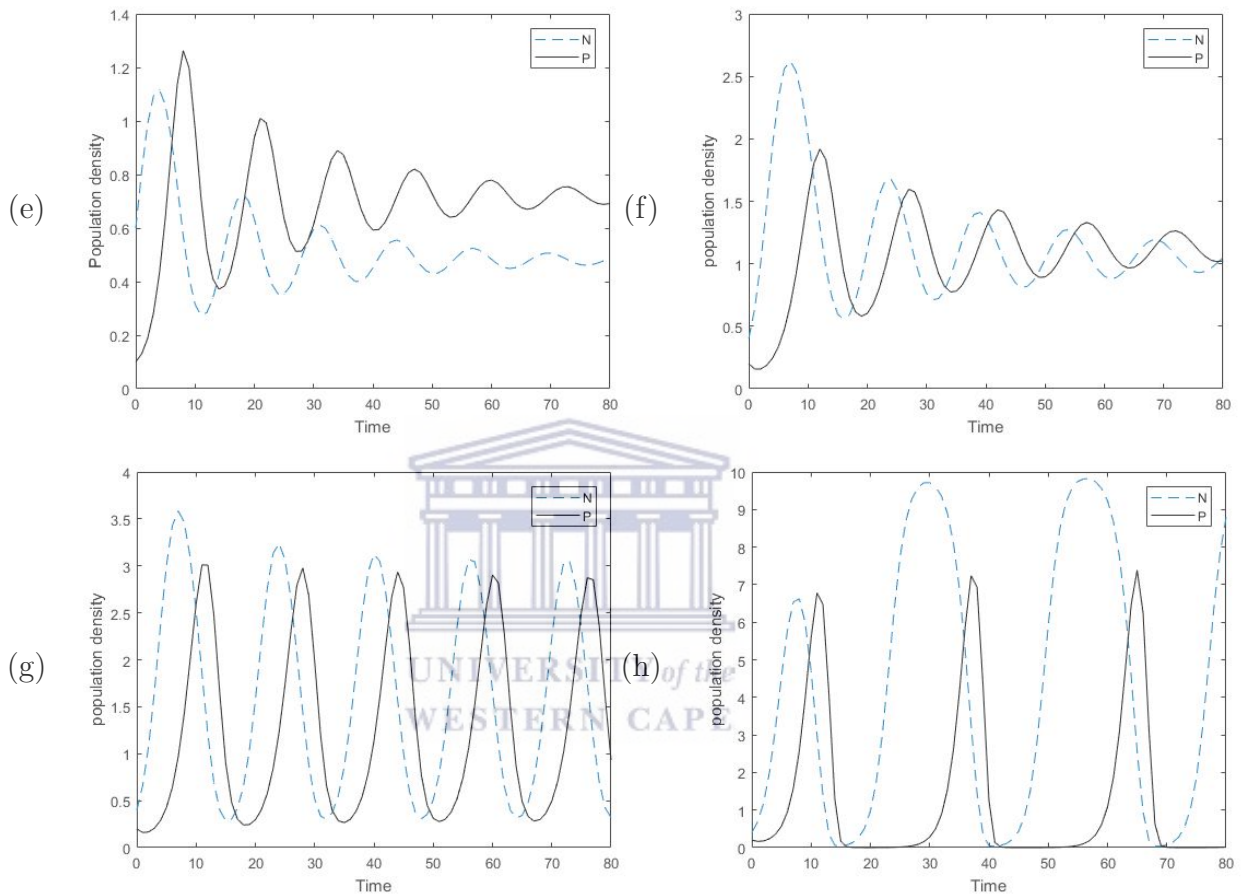


Figure 4.2: Solutions of the SSP model in time. The graph reflects different qualitative behaviors as the carrying capacity increases. A typical time-series behaviors of the two populations in one long-cycle period in which the paradox is resolved. In (e), (f), (g) and (h) only M changes while other parameters stay the same.

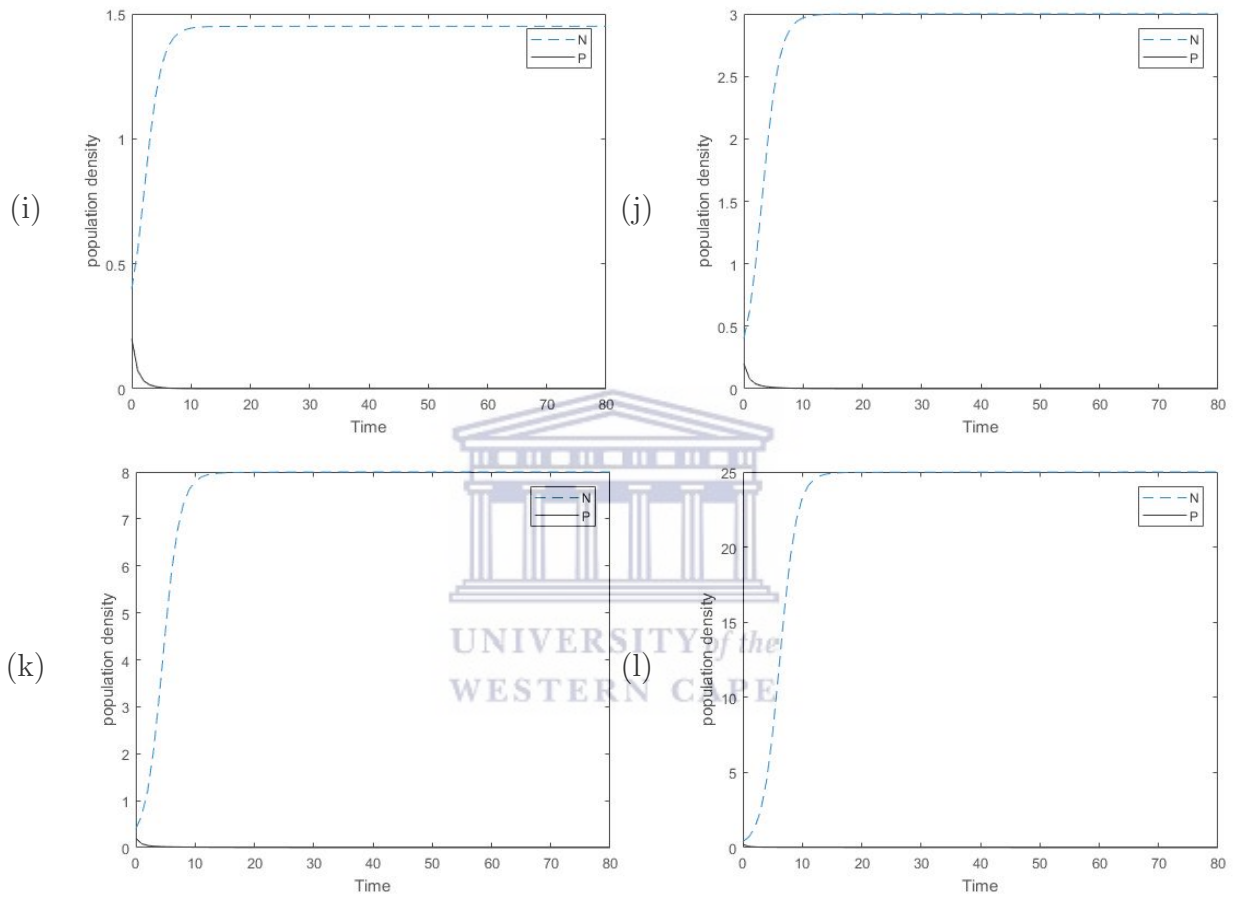


Figure 4.3: A possible behavior of two interacting species whereby extinction of the bacteria is highly possible. While other parameters stay the same, only M changes in (i), (j), (k) and (l).

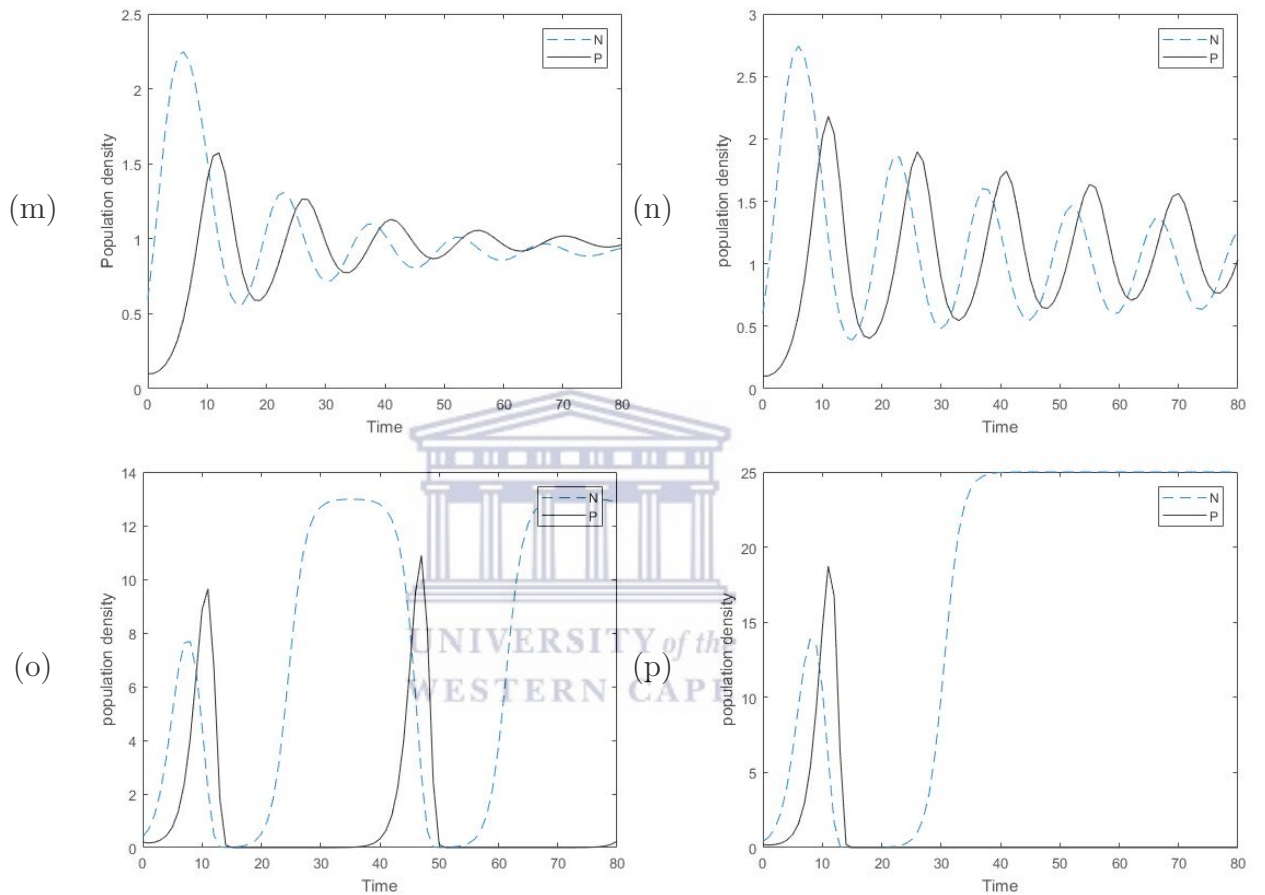


Figure 4.4: A strong possible retention of the nutrient population. The graph represents a non uniform oscillation system with long constant maximum and minimum intervals. In **(m)**, **(n)**, **(o)** and **(p)** only M changes while other parameters stay the same.

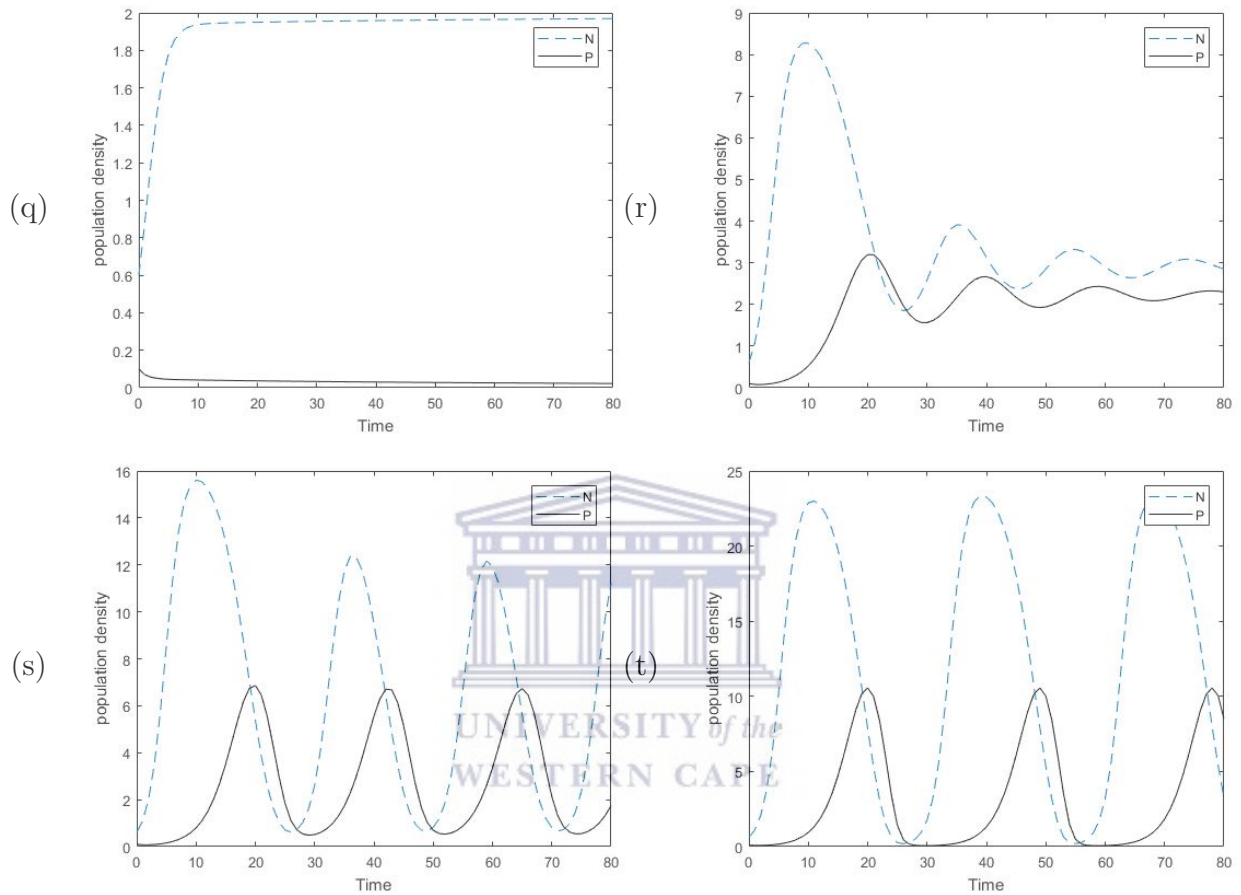


Figure 4.5: Solutions of the SSP model in time. The graph represents different qualitative behaviors as the carrying capacity M increased. (q) At $M = 2$, the SSP model takes two divergent points of view, with the nutrient increasing significantly to reach a maximum density of 1.95 when $t = 10$. Otherwise the nutrient population maintains a constant growth rate for all values of $t \geq 10$. The bacteria population declines to reach its lowest peak close to 0.1 at $t = 50$.

4.2 The results.

In this section, we give a general analysis of the SSP model with a positive paradox of enrichment status. The SSP model describes population densities of two species over a certain period of time. An observation has been made from the previous chapters as well as clearly shown in [18] of *Haque's* research studies that *enrichment* in interacting *predator-prey* dynamics resulted in more than one way of changing behavioral patterns completely. Thus, as *Murray* [40] pointed out, that would result in allowing the formation of new colonies or losing existing ones.

Giving a summary on the stability properties just about a *community equilibrium*, firstly make note that the *nutrient's* slope must almost always be negative for *local stability*. In [46] model, *Pimms* further argued that the greater the negativity of a prey slope the better and more stable the interactions would be. Otherwise in [57], *Wilson et al.* alluded that "*spatial structured patterns*" would move towards *instability*.

Quite interestingly, on one side, in [56] model, are the sequences of events, which includes the following

- (a) Reproduction and intra-specific competition followed by predation ($R \rightarrow P$),
- (b) Predation followed by reproduction and intra-specific competition ($P \rightarrow R$), and
- (c) Reproduction and intra-specific competition followed by predation. The last event depends on the prey population size prior to reproduction ($R \rightarrow P_D$).

Only in the last stage of [56], the sequence of events depended directly on the prey population size erstwhile to reproduction.

There are some interesting findings in the [56] model. The solutions presented altered behaviors with an increased carrying capacity K . The [56] model eventually reached a stable coexistence equilibrium point at $k = 1.4$ (an observation similarly displayed in Figure 4.1 (a) and Figure 4.3 (i) respectively). For the carrying capacity $k = 2.7$, the [56] model exhibited strong oscillatory coexistence along the invariant curve.

The paradox of enrichment had been obtained in [56] of *Weide et al's* model, when the invariant curve moved closer to one or both of the axes. Consequently, the coexistence

equilibrium in [56] lost its stability. As a result, all solutions of the system had strong oscillations. Henceforth, any increase in the carrying capacity then guaranteed existence of the *paradox of enrichment*.

However, while the [56] of *Weide et al.* model had a positive *paradox of enrichment* behavior, it had to some extent displayed different results. In the absence of a predator, the prey grew accordingly in line with the *BevertonHolt* equation. Concurrently, a non-vertical density hump for the bacteria had been established.

Conversely, the results in [41] of *Mougi-Nishimura* model, had a very negative *paradox of enrichment* due to a number of factors. To mention at least few such factors below:

- (i) An increased density of the less profitable prey together with that of enrichment subdued the oscillation amplitude of the predator with more profitable prey cycle.
- (ii) Consequently, that led to an insufficient suppressed amplitude which could not resolve the *paradox of enrichment*.
- (iii) This was due to its direct decrease in line with enrichment.
- (iv) Alternatively, the continued amplitude decrease was a result of the predator population enduring to utilise most of its time with only more profitable prey within the dynamics cycle.

An observation had been registered in [41] that for the *paradox of enrichment* to be resolved, the diet of the two predators should be the same. In such a case, there would therefore be high unfair competition that would result in an increased prey consumption rate. As a result, few effects of such a pattern had been noted in [41] results. Primarily, the less profitable prey functioned as a stable supplemental resource for the generalist predator. Subsequently, that led to a density decrease due to the presence of the specialist predator. Lastly, with high predation pressure due to two competitive species, there had been a substantial decrease in more profitable prey.

There are two main perspective factors which had made it possible for the stabilisation in [41] system of *Mougi-Nishimura* model. Namely,

- (i) On one hand, there must be consistent decrease in the amplitudes of oscillations.
- (ii) Contrary, an increase in all population densities of species involved must be

attainable.

Supplementary to [41]'s findings is that heterogeneity of predator types within trophic levels serves as a very significant factor for the resolution of *paradox of enrichment*. Hence, the following factors had been identified by the study in [41] to be of relevance:

- (a) Biodiversity plays an important role in the stability of ecosystems.
- (b) Dynamic-food web structures of complex interactions within species result to both the stability of system as well as resolving the *paradox of enrichment*.

Conversely, an increase in the carrying capacity M of the SSP model in Figure 4.1, resulted in a direct decrease to both amplitudes of the species.

Nevertheless, such a reflection does confirm the followings observations:

- (i) An existence of paradox of enrichment within the SSP model.
- (ii) The findings in (i) above are similar with both those in [56] of Weide et al. model and in [41] of Mougi-Nishimura model respectively and had been discussed in detail previously. There were no changes in the system for all simulations when $b < 2$. Only when $b = 2$ the entire system starts to drop the amplitudes significantly. The equilibrium points occurred when $b = 2.8$ with $t = 10.4$ and $t = 14.2$ respectively. Both populations were at 0.54 and 0.43 respectively.

On the other hand, any increase in λ had no effect on the amplitude of the system, a similar observation with other parameters mentioned previously. A decrease in λ had high effect on the amplitude, as it shifted the system very quickly to extinction (Figure 4.4 (p)). That occurred at a point where $b(1) = 0$ when $t = 3$ and $n(1) = 0$ as $t = 9$ correspondingly.

The behavior of the SSP model above $b = 3$ showed a change in the amplitude, hence reflecting more than five significant equilibrium points. Only at $t \geq 40$ did the system maintain constant oscillations, with both populations very close to 0.5 density. This result is more likely to retain more bacteria population compared to its nutrient. Lastly, an increase in both M and b resulted in a direct bacteria amplitude increase and a low nutrient decrease.

Chapter 5

Conclusion

Numerical simulation runs performed in the SSP model did confirm the linear theory. For a diverse chosen parametric values, the relevant partial differential equations of the SSP model displayed viable ecological oscillations. Accordingly, the reaction-diffusion system asymptotically had uniform oscillations with different amplitudes. Hence, the SSP model did confirm the results similar to those in [56] of Weide et al. and in [41] of Mougii-Nishimura correspondingly.

In the SSP model, a higher enrichment level did decrease the amplitudes of the short cycles. This is the same result that had been previously observed in [41] of *Mougii-Nishimura* model. The system also had a positive state of the *PoE* as the prey carrying capacity M increased. The presence of three equilibrium points in the SSP model is also very similar to those in [9] of Braverman model, in [56] of Weide et al. model and lastly to those in [47] of Rosenzweig-MacArthur model.

There is growing concern to institutions of conservation management as well as policy decision makers globally over the issue of *enrichment* as opposed by *Roy–Chattopadhyay* [51]. It is therefore based on this reason mentioned above that in [8]' model of *Bohannan–Lenski* had supported the *paradox's* subsequent effects in interacting *predator–prey* systems. Hence, according to *Murray* [39], applications of the *PoE* in mathematical modeling do advance the levels of planning, risk management and formulation of policy in invasion together with species that are at greater risk of extinction.

Several ecological studies reviewed including those in [41] of *Mougi-Nishimura* model and in [51] of *Roy -Chattopadhyay* model, confirmed that the *paradox* does really exist and is also possible to reverse it. A key challenging factor in many studies as *Haque* [18] cited, is that the *paradox of enrichment* had been left as unresolved effect allowing more space for further research opportunities.

Lastly, an existence of the *paradox* as highlighted in *Zhang et al.* [23], even though, according to *Xu-Li* [58], there had been counter arguments with regard to natural predation systems.



Bibliography

- [1] K. Krawczyk, W. Dzwiniel and D.A. Yuen (2003). Nonlinear development of bacterial colony modeled with cellular automata and agent objects. *Journal of Modern Physics C* vol. 30, pp 11-20.
- [2] R. Arditi and L.R. Ginzburg (1989). Coupling in predator-prey dynamics: Ratio-dependence. *Theoretical Population Biology*, vol. 139, pp 311-326.
- [3] R. Arditi, Y.Tyutynov, A. Morgulis, V. Govorukhin and I.Senina (2001). Directed movement of predators and the emergence of density-dependence in predator-prey models. *Theoretical Population Biology*, vol. 59, pp 207-221.
- [4] D.K Arrowsmith and C.M. Place (1992). Dynamical systems differential equations maps and chaotic behavior. *Chapman and Hall. Boundary Row, London SE18HN*.
- [5] A. Bazykin, A. Khinbnik and B. Krauskopf. Nonlinear dynamics of interacting populations. *World science*,
- [6] J.R. Beddington (1975). Mutual interference between parasites or predators and its effect on searching efficiency. *Journal of animal ecology*, vol. 44, no. 1, pp 331-340.
- [7] B. Courbau, G. Vellieledent and G. Kunstler (2010). Intra-specific variability and the competition-colonization trades-off: Coexistence, abundance and stability patterns. *Theoretical Biology*, vol. 5, pp 61-71.

- [8] B.J.M. Bohannan and B.E. Lenski (1999). Effect of prey heterogeneity on the response of a model food chain to resource enrichment. *The American Naturalist*, vol. 153, no. 1, pp 73-82.
- [9] L. Braverman, and E. Braverman (2009). Stability analysis and bifurcations in a diffusive predator-prey system. *Discrete and continuous dynamic systems*, pp 92-100.
- [10] B. Chen and M. Wang (2008). Qualitative analysis for a diffusive predator-prey model. *International Journal of Computational Maths and Applications*, vol. 55, pp 339-355.
- [11] R.L. Colasanti, R. Hunt and L. Watruda (2007). A simple cellular automaton model for high-level vegetation dynamics. *Ecological modeling*, vol. 203, pp 363-374.
- [12] D.L. DeAngelis, R.A. Goldstein and R.V. O'Neill (197). A model for trophic interaction. *Ecological society of America*, vol. 56, no. 4, pp 881-892.
- [13] Y. Du and S.B. Hsu (2004). A diffusive predator-prey model in heterogeneous environment. *Journal of Differential Equations*, vol. 203, pp 331-364.
- [14] H. Fujikawa and M. Matsushita (1989). Fractal growth of *Bacillus subtilis* on agar plates. *Journal of the Physical Society of Japan*, vol. 58, pp 3875-3878.
- [15] M. Genkai-Kato and N. Yamamura (1999). Evolution of mutualistic symbiosis without vertical transmission. *Theoretical Population Biology*, vol.55, pp 309-323.
- [16] M. Genkai-Kato and N. Yamamura (1999). Unpalatable prey resolves the paradox of enrichment. *The Royal Society*, vol. 266, pp 1215-1219.
- [17] C. Goodnight, E. Rauch, H. Sayama, M. A. M. de Aguiar, M. Baranger and Y. Bar-Yam. Evolution in Spatial Predator-Prey Models and the "Prudent Predator": The Inadequacy of Steady-State Organism Fitness and the Concept of Individual and Group Selection. University of Vermont, Burlington VT 05401, USA.

- [18] M. Haque(2011). A detailed study of the Bedding-DeAngelis predator-prey model. *Journal of Mathematical Biosciences*, vol. 234, pp 1-16.
- [19] E.E. Holmes, M.A. Lewis, J.E. Bank and R.R. Veit (1994). Partial Differential Equations in Ecology: Spatial Interactions and population dynamics. *The Ecological Society of America*, vol. 75, no.1, pp 17-29.
- [20] R.D. Holt and G.A. Polis (1987). A theoretical framework for intraguild predation. *The American Naturalist*, vol. 149, pp 745-764.
- [21] J. Huang, G. Lu and S. Ruan (2003). Existence of traveling wave solutions in a diffusive predator-prey model. *Journal of Mathematical Biology*, vol. 46, pp 132-152.
- [22] M.W. Hirsch and S. Smale (1974). Differential equations, dynamical systems and an introduction to chaos. *Academic Press of Pure and Applied Maths, New York-London*, vol. 60.
- [23] Z. Li, M. Gao, C. Hui, X. Han and H. Shi (2005). Impact of predator pursuit and prey evasion on synchrony and spatial patterns in meta-population. *Ecological modeling*, vol. 185, pp 245-254.
- [24] A. Ramanantoanina, C. Hui and A. Ouhinou (2010). Effects of density-dependent dispersal behaviors on the speed and spatial patterns. *Ecological Modeling*, vol. 222, pp 3524-3530.
- [25] F. Zhang, Z. Li and C Hui (2006). Spatio-temporal dynamics and distribution patterns of cyclic competition in meta-population. *Ecological Modeling*, vol. 193, pp 721-735.
- [26] V. Hutson, Y. Lou and K. Mischaikow (2002). Spatial heterogeneity of resources versus Lotka-Volterra dynamics. *Journal of Differential Equations*, vol. 185, pp 97-136.

- [27] V.A.A. Jansen (1995). Regulations of predator-prey systems through spatial interactions: A possible solution to the paradox of enrichment. *Nordic Society Oikos*, vol. 74, no. 3, pp 384-390.
- [28] V.A.A. Jansen and A.L. Lloyd (2000). Local stability analysis of spatially homogeneous solutions of multi-patch systems. *Journal of Mathematical Biology*, vol. 41, pp 232-252.
- [29] Jordan and Smith, P.J. Oliver (1992). Dynamics and the geometry of behavior. *Hindustan publishers* vol 2.
- [30] C.X.J. Jensen and L.R. Ginzburg (2005). Paradoxes or theoretical failures? The jury is still out. *Ecological modeling*, vol. 188, pp 3-14.
- [31] K. Kawasaki, A. Mochizuki, M. Matsushita, T. Umeda and N. Shigesada (1997). Modeling spatio-temporal patterns generated by *Bacillus subtilis*. *Journal of Theoretical Biology*, vol. 188, pp 177-185.
- [32] D. Bontje, B.W. Kooi, G.A.K. van Voorn and S.A.L.M Kooijman (2009) . Feeding threshold for predators stabilises predator-prey systems. *Mathematical models of natural phenomena*, vol. 4, no. 6, pp 91-108.
- [33] W. Ko and K. Ryu (2007). Coexistence states of a predator prey system with non-monotonic functional response. *Nonlinear Analysis: Real world Applications*, vol 8, pp 769-786.
- [34] Y.H. Lee, L. Sherbakov, J. Taber and J. Shi (2006). Bifurcation diagrams of population models with nonlinear, diffusion. *Journal of Computational Applied Mathematics*, vol. 194, pp 357-367.
- [35] E. McCauley and W.W. Murdoch (1990). Predator-prey dynamics in environments rich and poor in nutrients. *Nature*, vol. 343, pp 455-457.

- [36] E.McCauley, W.G.Wilson and A.M. De Roos (1993). Dynamics of age-structured and spatial structured predator-prey population interactions: Individual-based models and population level formulations. *The American Naturalist*, vol. 142, no. 3, pp 412-442.
- [37] J.M. McGlade (1999). Advanced Ecological Theory: Principles and Applications. *Journal of Blackwell Scientific Publications, Oxford*.
- [38] I.S.Molchanov (2006). Diffusion limited aggregation with jumps and flights. *Journal of Statistical Computation and Simulations*, vol 64, pp 357-381
- [39] J.D. Murray (2002). Mathematical biology I: An introduction, 3rd edition. *Interdisciplinary Applied Mathematics*, vol. 17.
- [40] J.D. Murray (2003). Mathematical Biology II: Spatial models and biomedical applications, 3rd edition. *Journal of Interdisciplinary applied Mathematics*, vol 18.
- [41] A. Mougi, and K. Nishimura (2007) . A resolution of the paradox of enrichment. *Theoretical Biology, Springer Science and Business Media*, vol. 248, pp 194-201
- [42] A. Mougi and K. Nishimura (2008). Imperfect optimal foraging and the paradox of enrichment. *Theoretical Ecology, Springer Science and Business Media*, Original paper, pp 1-7.
- [43] A. Mougi and K. Nishimura (2008). The paradox of enrichment in an adaptive world. *Proceedings of The Royal Society of Biology*, vol. 275, pp 2563-2568.
- [44] A. Okubo and S.A. Levin (2001). Diffusion and ecological problems: Modern Perspectives. *Springer, New York*, pp 30-106.
- [45] E.C. Pieluo (1969). An introduction to mathematical ecology. *John Wiley and Sons publication*,
- [46] S.L. Pimms (1991). The balance of nature? Ecological issues in the conservation of species and communities. *The University of Chicago Press*.

- [47] M.L. Rosenzweig and R.H. MacArthur (1963). Graphical Representation and stability conditions of predator-prey interactions. *The American Society of Naturalist*, vol. 97, no. 895, pp 209-223
- [48] M.L. Rosenzweig (1971). Paradox of enrichment: Destabilization of exploitation ecosystems in ecological time. *Journal of Science, New Series*, vol. 171, no. 3969, pp 385-387.
- [49] M.L. Rosenzweig (1995). Species diversity in space and time. *Cambridge Univ. Press*, pp 343-348.
- [50] P. Rohani, R.M. May and M.P. Hassel (1996). Meta-populations and equilibrium stability. The effects of spatial structures. *Journal of Theoretical Biology*, vol. 181, pp 97-109.
- [51] S. Roy and J. Chattopadhyay (2007). The stability of ecosystems. A brief overview of the paradox of enrichment. *Journal of Biological Science*, vol. 23, pp 421-428.
- [52] B.K. Singh, J.S. Rao, R. Ramaswamy and S. Sinha (2004). The role of heterogeneity on spatio-temporal dynamics of host-parasite meta-population. *Ecological Modeling*, vol. 180, pp 435-443.
- [53] D. Tilman (1980). A Graphical Mechanistic Approach to Competition and Predation. *The American Naturalist*, vol. 116, no. 3, pp 362-393.
- [54] M. Vos, B.W. Kooi, D.L. DeAngelis and W.M. Mooij (2004). Inducible defenses and the paradox of enrichment *Wiley-Blackwell and Nordic Society Oikos*, vol. 105, no.3, pp 471-480.
- [55] P.J. Wangersky and W.J. Cunningham (1957). Time-lag in prey-predator population models. *Ecological society of America*, vol. 38, no. 1, pp 136-139
- [56] Weide, Vinicius; Varriale, Maria C.; Hilker, Frank M. Hydra effect and paradox of enrichment in discrete-time predator-prey models. *Math. Biosci.* 310 (2019), 120127.

- [57] W.G. Wilson, A.M. DE Roos, and E. McCauley (1993). Spatial instabilities within the diffuse Lotka-Volterra system: Individual based simulation results. *Theoretical Population Biology*, vol. 43, pp 91-127.
- [58] C.L. Xu and L.Z. Li (2002). Effect of diffusion and spatially varying predation risk on the dynamics and equilibrium density of a predator-prey system. *Journal of Theoretical Biology*, vol. 219, pp 73-82.
- [59] Y. Wu, and X. Zhao (2005). The existence and stability of traveling waves with transition layers for some singular cross-diffusion systems. *Science China Mathematics*, vol. 53, no. 5, pp 1161-1184.
- [60] X.Q. Zhao (2003). Dynamical Systems in Population Biology *Science China Mathematics*, Springer, New York, vol. 16.

