Mathematically Modeling the Interactions Between Phages, Bacteria, and the Environment

MSc Thesis *(Afstudeerscriptie)*

written by

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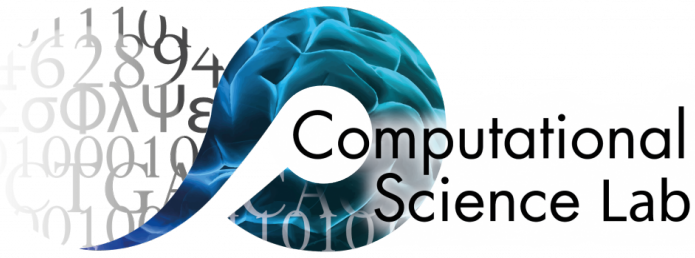

Abstract

Abstract text here

Abbreviations of terms

Abbreviations	Full Word
ODE/s	Ordinary Differential Equation/s
DDE/s	Delay Differential Equation/s
PDE/s	Partial Differential Equation/s
BVP	Boundary Value Problem
ABM/s	Agent Based Modelling/Models
-	-

Contents

1 Introduction

Phages, small viruses that infect, replicate, and kill bacteria, are nature's natural anti-microbial defense. Research is currently being done to determine the applications of phages in controlling bacterial infections and spread. Phages have applications in human and animal health. Phage cocktails are a type of medicine for sick patients with bacterial diseases, such as *E. coli*. A patient can intake a pill filled with specific phages that target *E. coli*. The phages will target the specific *E. coli* bacteria, but will not affect the other bacteria and will not have any side effects on the body. There are 100 trillion microbes across 5,000 different types of bacteria strains in the human gut. Using medicine such as antibiotics can disrupt the intricate ecosystem of the gut microbiome, acting as a scorched-earth mechanism. Phages on the other hand specifically target a specific bacterial strain, acting as a sniper, with minimal to no effects to other bacteria. This can be used to control bacterial infections and cure people, or to prevent the spread of common bacteria in livestock, which are commonly raised in tight spaces with a lack of sanitation facilities to clean out the feces and other junk of the livestock.

Phages have applications in the food production business. Once an animal is slaughtered, bacteria start to grow and eventually spoil the meat. A possible way to prolong the shelf-life of meat is to use a solution of water with a mixture of phages and douse the meat with the solution. As the bacteria start to replicate, the phages kill the bacteria, slowing the growth down. An issue with this is that there are many types of bacteria, while phages can only target a select few bacteria strains.

In an ecosystem like the ocean, the gut, or in soil, there are thousands of different microbes. The ecosystem is complex, with many factors affecting the growth of bacteria, fungi, phages, and more. External factors, such as flooding, droughts, or chemical spills have a massive impact on the ecosystem, adding or removing nutrients from the system, a change in temperature and pH of the ecosystem, or directly destroying microbes. These effects can affect the balance of microbes, affecting the larger ecosystem and food chain as a whole. For example, bacteria are used to decompose dead organic material into nutrients for the grass to grow, which is then eaten by rabbits who are eaten by eagles.

Not much is known about phages in large and complex communities between other phages, bacteria, resources, and the environment. There have been previous attempts to model the complex dynamics of the populations between phages, bacteria, and resources, with the environment using Ordinary Differential Equations(ODE) and Delay Differential Equations (DDE). However, these methods have mainly stayed with 1-to-1-to-1 models, meaning 1 phage, 1 bacteria, and 1 resource. Other methods such as Partial Differential Equations (PDE) or cellular models have been created in an attempt to model these types of dynamics. There are two main ways to model phage-bacteria dynamics: a spatial model or a non-spatial one. A spatial model means that phages and bacteria can travel through space, while with non-spatial models the bacteria and phages are assumed to be in a well-mixed solution. Special considerations have to be

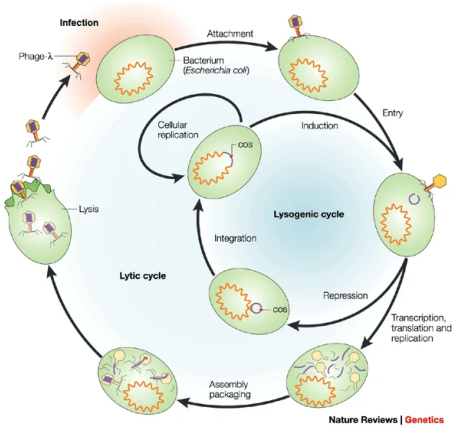

Figure 1: Life cycle of a phage inside and outside a bacteria cell.

accounted for with spatial models. Bacteria and phages can only interact in the proximity of one another, while in non-spatial models it is assumed that a set percentage p interact with one another. Spatial models can potentially lead to more interesting and complex results but are limited to smaller populations and harder to develop, while non-spatial models are easier to develop and are more effective in modeling large populations. PDE and cellular models are types of spatial models, while ODEs and DDEs are types of non-spatial models

1.1 Biological Background

Phages are small viruses on the order of 27-190 nm that infect and lysis (kill) specific bacteria. The phage cycle process starts by a phage coming into contact with a bacterium. Once it has identified an injection site, the phage can inject a strain of DNA into the bacteria. The DNA strand has two options, either it can merge into the DNA of the bacteria, so that when the bacteria replicate, the phage's DNA strand is replicated along with the bacteria. This stage is called the Lysogenic Cycle. After a set amount of time, the DNA of the phage can unmerge and hijack the DNA replicating mechanism, creating multiple copies of itself, using the transcription, translation, and replication process to create multiple copies of itself. The phages begin to self-assemble inside the bacteria until the bacteria is full of phages and explodes, the lysing stage, releasing the phages into the environment, ready to repeat the process again.

This process can be visualized in Figure 1. [2]

1.2 Real World Applications of Phages

Due to the nature of killing bacteria, there are numerous applications where a researcher or an organization might be interested in controlling bacterial popu-

lations. A Food Safety Specialist might be interested in introducing a solution containing a high concentration of phages during food production to prevent the spread and growth of *Salmonella* or *E. coli*, without affecting the quality of the food that other bacterial control methods like heat or acidity provide. The Food Safety Specialist might want to promote beneficial bacteria like *Streptococcus thermophilus* used in the production of Emmantal cheese, which heat would also kill. A doctor might be interested in providing swallowable pills, more commonly known as phage cocktails, to a patient with a bacterial infection. The medication can contain any number of different phages that can target specific bacterial infections such as *Streptococcus pneumoniae* with minimal risk of side effects. An Environmental Protection Officer might be interested to see how they can use phages to stop the spread of *Cyanobacteria* blooms in waterways, more commonly known as blue-green algae, a photosynthetic microscopic organism that is technically a type of bacteria. This would keep waterways safe for boating and swimming activity, aquatic life, and water consumption in farms, factories, and homes.

1.2.1 Controlling Foodborne Bacteria

Foodborne diseases are one of a few primary ways for bacteria to spread to humans and animals. Some bacteria directly infect the host, while some bacteria will deposit toxins on the food. If consumed in large enough quantities, the toxins can be fatal. Methods exist to control bacterial growth, for example by storing food below 5C or above 60C. Bacteria need moisture to grow, so starches like rice will have minimal bacterial growth. Bacteria prefer to live in slightly acidic to neutral pH environments, so having an environment that is extremely acidic like vinegar will prevent bacterial growth. The use of chemical antibacterial agents such as bleach are not desirable due to leaving chemicals on the food, which can be fatal if ingested. Physical agents like heat or radiation can kill bacteria, but at the cost of altering the food quality [6].

1.2.2 As an Alternative to Antibiotics

1.2.3 Environmental Protection

Algae blooms, also called red tides, is the rapid spread of bacterial or algae organisms. Blooms are a growing environmental concern impacting water quality, aquatic ecosystems, and human health. These rapid increases in algae populations, often fueled by excess nutrients like nitrogen and phosphorus, can occur in freshwater, coastal, and marine environments. Algae can produce toxins that threaten wildlife, contaminate drinking water, and disrupt local economies dependent on fishing and tourism. In the state of Florida, between the years 1995 and 2000, an estimated $6.5 million was lost in the restaurant and hotel industry due to algae blooms. This accounts for about 25% of the average total monthly sales revenue in the region from June through October, the months that are most commonly affected by red tide[1]. During a red bloom event, hospital diagnoses in the county of Sarasota for pneumonia, gastrointestinal, and

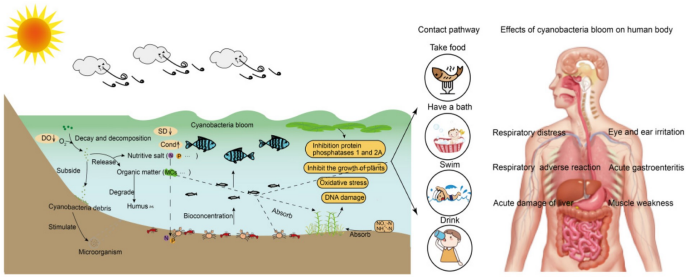

Figure 2: Cyanobacteria degradation cycle, main hazards of cyanobacteria bloom to water bodies, aquatic organisms, and the human body. (DO: dissolved oxygen; SD: water transparency; Cond: conductivity; N: nitrogen; P: phosphorus; MCs: microcystins). [15]

respiratory illness increased by 19%, 40% and 54% respectively [3, 9], with a respiratory illness visit costing between \$0.5% and \$4 million [8].

Cyanobacteria blooms have major effects on the aquatic environment as well as human health. Cyanobacteria release nitrogen and phosphorous, which the bacteria use to grow with oxygen, outpacing other aquatic growth, and killing aquatic marine life. Toxins can make their way into the food and water consumed by humans, causing muscle fatigue, respiratory issues, liver damage, and gastrointestinal issues [15]. Figure 2 shows the process of how cyanobacteria degrade and are absorbed into the environment, eventually making their way into the human body via various contact points.

2 Literary Review

2.1 Methods of Modelling Phages and Bacteria

There are numerous ways to model the interactions between phages and bacteria. Models can be built at a molecular level, where the model simulates the mechanical and chemical behavior of a phage as it interacts with the surface of a bacterium using computational chemistry methods. On the other end of the spectrum, a different type of model can be built where populations of phages, bacteria and bacteria can be modeled using Ordinary Differential Equations (ODEs) or Delay Differential Equations (DDEs). DDEs are similar to ODEs, except where when ODEs are calculating the values of the equations at time t using time $t-1$, DDEs can, but don't have to, use the value of the equation at time $t-\tau$, where $1 \leq \tau \leq t$.

Each type of system has its pros and cons. With the molecular level model, the model is more complex and needs significantly more startup time, simulation time, and is in general much more complex. However, more information can be gained from the simulations and can guide research in creating phages for a certain type of bacteria. The ODE method is simpler and easier to set up, however it can only capture large population dynamics. Certain assumptions have to be made, for example ω percent of the bacteria population is washed out. The model can be made more complicated, by modelling each stage of a lysis, or when calculating the washout rate of bacteria, use a normally distributed variable $\mathbf{N}(\mu = \omega, \sigma = 1)$ to capture slight variations in a parameter at each step to controllably randomize parameter values to capture noise in measuring data. Ensuring the use of a seed value will ensure that each run of the model results in the same output.

2.1.1 Generalized Lotka-Voltera Model

The Lotka-Voltera model, a first-order non-linear differential model is a model that captures the dynamics between predators and prey, with phages being the predator and bacteria being the prey. Any population can be modelled as such

$$\frac{dB_i}{dt} = B_i \left(\left(r_i + \sum_j^N \alpha_{ij} B_j \right) - m_i \right)$$

where ...

2.1.2 Generalized Consumer-Resource Model

The generalized Consumer-Resource Model models the growth of a population and resource dynamics between a population of bacteria B_i and a resource R_i.

$$\frac{dB_i}{dt} = r_i B_i \left(\sum_{\alpha} \Delta w_{i\alpha} C_{i\alpha} R_\alpha \right) - m_i B_i \tag{1}$$

$$\frac{R_\beta}{dt} = -\sum_{i} C_{i\beta} R_\beta B_i + \sum_{\alpha,i} D^i_{\beta\alpha} C_{i\alpha} R_\beta B_i \tag{2}$$

$$\Delta w_{i\alpha} = \sum_{\beta} D^i_{\beta\alpha} w_\beta \tag{3}$$

2.1.3 Trait-Based Model

The Trait-Based Model is a model that takes into account external factors such as the temperature or pH of the system, and can be modeled as following:

$$\frac{dB_i}{dt} = (r_i - m_i) B_i \tag{4}$$

$$r_i = \frac{r^{max}_{i\alpha} R_\alpha}{R_\alpha + K_{i\alpha}} e^{S_i (T - T_{ref})} \tag{5}$$

where S_i is the sensitivity to B_i to factor T, and with tradeoff if $r_i^{max} >$ mean r^{max} then $S_i >$ mean S.

2.1.4 Agent-Based Models

Agent-based Models (ABM) model the system through space and time. An $x \times y \times z$ grid (often z is left out for a 2D system) is created and split into smaller subcells containing resources and microbes. Each cell acts as its own tiny environment, where resources and microbes interact within the environment, but not with the neighboring cells. Resources are diffused through the system using a PDE solver for a Boundary Value Problem (BVP). Agents are allowed to move into neighboring grids with a probability p, where p can depend on any number of parameters such as nutrient density, microbe density, or stochastic chance.

ABMs are useful when simulating many individual elements interacting in a system. Chaotic or emergent behaviour can arise from these interactions. Chaotic behavior refers to the irregular and unpredictable evolution of a system's behavior due to nonlinear equations, exhibiting sensitive dependence on initial conditions [12].

Emergent behavior is something that is a nonobvious side effect of bringing together a new combination of capabilities—whether related to goods or services. Emergent behaviors can be either beneficial, benign, or potentially harmful, but in all cases they are very difficult to foresee until they manifest themselves. Agents can have simple rules, but when interacting with other agents, behavior

that hasn't been programmed can arise. Emergent behaviors are also sometimes considered to be systems that are more complex than the sum of their parts [11].

$$\frac{\delta R_\alpha(r,t)}{\delta t} = \nabla \left[D\left(R_\alpha, r\right) \nabla R_\alpha\left(r,t\right) \right], r = (x,y) \tag{6}$$

. The cellular agents rules are as follows.

$$\frac{di}{dt} = r_i \left(\sum_\alpha \Delta w_{i\alpha} C_{i\alpha} R_\alpha \right) \tag{7}$$

, where if $i >$ threshold, $\frac{i}{2}$ expands into the neighboring grid cell with a probability p. The resource consumption and conversion into new sub-resource types are described as follows.

$$\frac{dR_\alpha}{dt} = -\sum_i C_{i\alpha} R_\alpha I \tag{8}$$

$$\frac{dR_\beta}{dt} = \sum_i C_{i\beta} R_\beta I + \sum_{\alpha,i} D^i_{\beta\alpha} C_{i\alpha} R_\alpha i \tag{9}$$

2.2 Biology of Phages

2.2.1 Current Applications: Food Control

When there are small number of known bacterial strains, a targeted concoction of phages can be used to control the bacterial population growth on the food. Phages offer properties of microbial control that other methods do not. Phages do not modify the food quality and do not leave behind harmful chemical residues. Phages are hyperspecific to the bacteria that they can kill, and they don't affect other beneficial bacteria. For example, *Streptococcus thermophilus* is one of three different bacteria strains used to create emmental cheese. However, Emmental cheese does not use pasteurized milk, increasing the risk of *E. coli*. Emmental cheese producers can add phages that target *E. coli* to the milk during the production stage while not affecting the bacteria used to produce the cheese.

Phage cocktails like SalmoFresh$^{\text{TM}}$ have been proven to safely reduce *Salmonella* contamination in pet food and raw pet food ingredients [13], as well as in romaine lettuce and bean sprouts [16]. Pet food contains meat and vegetables, where vegetables grown in or on the ground are at risk of *Salmonella* due to contact with soil, manure, compost, and other agricultural runoff from neighboring farms [10]. Figure 3 [13] and Figure 4 [16] show how applications of phages have reduced the count of *Salmonella* in ingredients used in pet food as well as romaine lettuce and bean sprouts. As such, phages can be shown to control the spread of *Salmonella* in food sources.

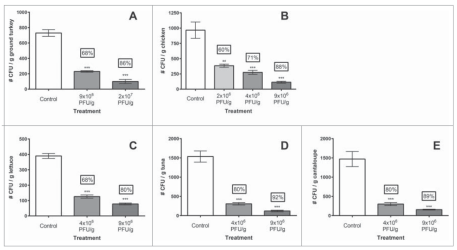

Figure 3: SalmoLyse® reduces Salmonella contamination on various food surfaces: Mean and standard error bars shown. Statistical analyses were carried out for each food group independently. Asterisks denote significant reduction from corresponding controls based on one-way ANOVA with Tukey's post-hoc tests for multiple corrections: ** denotes $p < 0.01$, while *** denotes $p < 0.001$ compared to the corresponding controls. There was significant reduction in Salmonella on all food surfaces with the addition of SalmoLyse® compared to the controls; the mean percent reductions from the control are noted in the boxes above treatment bars. CFU/g D colony forming units per gram. Each letter denotes a food group that was tested with SalmoLyse® and compared to a control: A= chicken; B= lettuce; C= tuna; D= cantaloupe; E= ground turkey. [13]

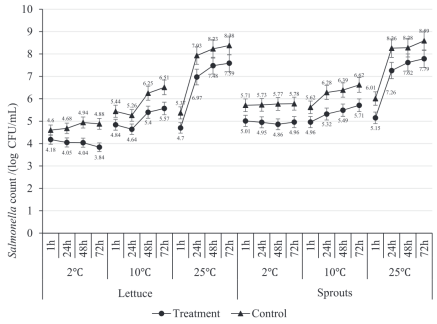

Figure 4: *Salmonella* count in a mixture of 5 *Salmonella* strains spot-inoculated (CFU/g) onto a) lettuce and b) sprouts after spraying with a mixture of bacteriophage (SalmoFresh™) relative to positive controls at 2, 10 and 25C and stored for 1, 24, 48 and 72 h. [16]

2.2.2 Current Applications: Bacterial Infection Control

2.2.3 Current Applications: Environmental Control

There is interest in using phages to control cyanobacteria blooms. Phages can offer better and safer options than chemical options. Chemical options are indiscriminate, killing cyanobacteria, while also killing other beneficial bacteria and aquatic life. Although not used to control bacteria blooms, some chemicals like PFAS, also called "Forever Chemicals", can last a long time in the environment and don't degrade and keep on negatively affecting the environment. Due to the specificity of phages, only the cyanobacteria will be targeted, and will not affect the surrounding areas. Tucker and Pollard found that an isolated phage cocktail collected from Lake Baroon in Australia could decrease the abundance of *M. aeruginosa* by 95% within 6 days in a lab setting, before recovering within 3 weeks time [14].
There is evidence that phage-resistant bacteria can influence the population dynamics of other bacteria. It has been shown that the plankton level has been experimentally affected by the frequency of the phage-resistant *Nodularia* marine bacteria. Populations with high phage resistance ($> 50\%$) dominate the plankton communities despite a high phage count and eventually outcompete other bacteria due to their slower loss in population count. Contrastingly, populations of bacteria with low phage resistance (between 0% and 5%) were lysed to extinction, releasing nutrients like nitrogen. This allows for other bacterial strains to absorb the nutrients and dominate the bacterial community. Phages and the lysis of bacterial strains can have a dramatic effect on community dynamics and composition of other agents like phages, bacteria, and resources [4]. Phages have the potential to be used as a highly specific strategy for the control of cyanobacterial blooms, with minimal effects to the environment, and offer control bacterial blooms, with limited impact to the environment. Usage should be relatively safe, novel, efficient, and sensitive.

However, there are issues with using phages to control bacterial blooms. Bacterial blooms can cover vast areas, or be in areas that would be hard to reach like marshlands, applying phages to combat the bloom might be infeasible. If the method of choice was to spray a solution of water containing phages, the solution needs to be shipped to the site and loaded onto special boats to spray the solution into the water, or the trucks need to drive along the shore and spray the solution into the water. The phage density in the solution will have to be relatively high to quickly combat the bloom. These problems provide major logistical problems with creating the phages in a lab or factory, transporting the phages, and finally the administration of the phages to the waterways. Phages can only diffuse through the water, and can't actively swim, so they are dependent on the rate of diffusion and water currents. This will be difficult in marshlands, where the bacteria can "hide" in the grass and crevices created by aquatic life. If the bloom is in a high current area, like in a river or a bay, the water can wash the phages away. On top of that, The infection mechanism of

phages is not exactly known, and research into artificial engineering of phages is not in-depth, making it harder to do research in this area [7, 5].

3 Methods

3.1 Network Topography of Interactions

In a microbial environment, there are numerous interactions between agents, but not every agent can and will interact with one another. Based on which agents interact with which agents, a network topography can be created, capturing the dynamics of the interactions. Each agent can be represented as a node. If an agent interacts with another agent, an edge can be linked between the agents. Each node can contain attributes and properties related to that agent, for example starting population or concentration, washout rate, or birth rate. Each edge likewise also contains attributes to capture the dynamic interactions between the agents, for example, resource usage, burst size, or affinity to infect. Adding the attributes to the nodes and edges allow for various The parameters can change between agents. For example, the initial population of phage 1 can be 300, while for phage 2 it is 150. Likewise, the attributes can be different between different agents. For example, bacteria 1 might use up resource 1 with rate constant 0.05, while bacteria 1 might use up resource 2 with rate constant 0.07. Bacteria 2 might not need resource 1 to survive, but bacteria 2 requires a lot of resource 2 to grow, with usage rate constant of 0.4. Using a graph network, these interactions between agents can be visualized, tracked and edited.

A tool has been developed to help aid in the development of this network topography. With this tool, a network topography can be created by adding any number of agents of varying type, such as bacteria, phages, or resources. There is an optional environment node that can capture global environment data, for example the length of the simulation, number of timesteps, temperature, pH, etc. The attributes of the agents, interactions, and environment can easily be edited.

Once a network topography capturing the interactions between any number of agents has been created, it would be useful to see how the population count or concentration value changes through time. A Python package has been created that allows for uploading a network topography, and with a small script that the user needs to provide, with the setting up of initial parameters and provided equations, runs a numerical solver using SciPy's solve_ivp() function.

4 Experiments and Results

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5 Discussion

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6 Conclusion and Future Work

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A Parameters

Parameters used in equations

Parameter	Parameter Full Name	Description	Default Value	Alternatives	Notes
P	Phage Parameter	Phage population count			
U	Unifected Parameter	Uninfected bacteria population count			
I	Infected Parameter	Infected bacteria population count			
R	Resource Parameter	Resource concentration			
B	Bacteria Parameter	Bacteria population			Some mo
ω	Washout Rate	Rate of parameter washing or flowing out of the system			
β	Burst Size	Number of phages created when bacteria cell bursts			
t	Time	Time step during simulation			
μ	Mean	Mean			
σ	Standard Deviation	Standard deviation			
T_{min}	Minimum Temperature	Minimum operating temperature for a microbe			
T_{opt}	Optimal Temperature	Optimal operating temperature for a microbe			
T_{max}	Maximum Temepra-ture	Maximum operating temperature for a microbe			
pH_{min}	Minimum pH	Minimum operating pH for a microbe			
pH_{opt}	Optimal pH	Optimal operating pH for a microbe			
pH_{max}	Maximum pH	Maximum operating pH for a microbe			

B Appendix 1

Appendix 1 text