Wave Solutions of Nonlocal Delayed Reaction-Diffusion Equations

by

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Abstract

Appearance of waveforms in population dynamics is a key element in studies of single and interacting species. The present work considers an age-structured model for single species that is in the form of a nonlocal delayed Reaction-Diffusion (RD) equation. The local and global stability of steady states are investigated as an intrinsic part of the wave studies. This is carried out through standard techniques such as linearization, Liapunov functionals and the method of characteristics. The present work differs from a large number of recent wave studies in two important respects. First, in contrast to several studies focused on the existence of the wave solutions, the emphasis is on the development and implementation of techniques for construction of the wave solutions. Secondly, it is not limited merely to the traveling wavefronts of the model but instead explores traveling and stationary wave solutions in the form of fronts and pulses. Considering wave solutions in such a broad context can reveal underlying physical and biological mechanisms that play crucial roles in dynamics of single species populations. Here, employing specific birth functions in the model, stationary wavefronts and wave pulses are obtained through an energy function method. By means of a number of techniques such as boundary layer and asymptotic expansion, the traveling wave solutions of the model are approximated. Although the age-structured model takes into account various key elements such as nonlocality and delay, it considers the unbounded one-dimensional domain. The present work also develops the model with respect to two-dimensional spatial domains. This enables further comparison between the outcomes of the model and those of laboratory experiments.

To Grace, Jose and Victoria

Acknowledgments

I would like to thank my supervisor Dr. David E. Amundsen for his time and patience and for giving me the opportunity to work in the field of mathematical biology. I want to thank my wife for being supportive and encouraging me to continue my studies. I am so grateful to my parents who have been continuously helping me to achieve my goals in life. God bless both of them!

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Chapter 1

Delay Models and Wave Solutions

A primary objective of the present chapter is to provide a succinct review of the well-known models of population dynamics and the behavior of their waveform solutions. This has been supported with numerical analysis of certain delay and non-delay models that have been frequently used in various studies. This review is intended to provide enough background and rationale to state the main problem of this work. The contents of this chapter are organized as follows. Section 1.1 is a short introduction to the theory of Retarded Functional Differential Equations. This is followed by analysis of some delay models that have been used in studies of various single species populations. Section 1.2 is an introduction to traveling wave solutions. Wave solutions of delay and non-delay linear Reaction-Diffusion (RD) equations as well as those of Fisher-Kolmogoroff models are investigated in depth. Section 1.3 delves into model extensions and the concepts of diffusion and nonlocality in population models. Finally, Section 1.4 delivers the statement of the main problem. The present work is a treatment of a recent nonlocal RD model with respect to stability of steady states, wave solutions and two-dimensional model extensions.

1.1 Functional Differential Equations: Theory and practice

Application of Delay Differential Equations (DDEs) in modeling different biological situations has been on a rapid ascension. A simple example arises due to the fact that the population density of a single species is directly dependent on the food resources. A shortage in the resources takes time to be resolved which can result in fluctuations in population growth or even in extinction of the entire population. Another example emerging in nature is reforestation. After replanting a hewn forest, it will take a minimum of twenty years for trees to reach any level of maturation. Hence, any reforestation model without delays is an approximation at best.

Systems of Ordinary Differential Equations (ODEs) and Partial Differential Equations (PDEs) without delay are governed by the principle of causality; that is, "the future state of the system is independent of the past and is determined solely by the present" [91]. In various situations a model is realistic if it includes some of the past history of the system. Therefore, in systems of DDEs, the derivative at any given time depends on the solution at prior times. Let us formulate this mathematically. Suppose $r \geq 0$ is a given real number, $C([-r,0],\mathbb{R}^n)$ the Banach space of bounded continuous functions $\phi : [-r,0] \to \mathbb{R}^n$ with norm $\|\phi\| = \sup_{-r\leq\theta\leq 0} |\phi(\theta)|$ and suppose $F : \mathbb{R} \times C([-r,0],\mathbb{R}^n) \to \mathbb{R}^n$ is a given mapping, then

$$\dot{x}(t) = f(t, x_t), \tag{1.1}$$

is called a Retarded Functional Differential Equation (RFDE) where $x_t \in C((-r,0),\mathbb{R}^n)$ and for any $t \in [a, a+b], a \in \mathbb{R}, b \geq 0$ is defined by

$$x_t(\theta) = x(t+\theta), \tag{1.2}$$

with $-r \leq \theta \leq 0$ and $x \in C([a-r, a+b],\mathbb{R}^n)$.

For any given $\sigma \in \mathbb{R}$, $\phi \in C$, we say that $x(\sigma,\phi,f)$ is a solution of equation (1.1) with initial value ϕ at σ. Equation (1.1) includes ODEs by letting $r = 0$,

$$\dot{x}(t) = f(t, x(t)), \tag{1.3}$$

Retarded Differential Difference Equation (RDDE)

$$\dot{x}(t) = f(t, x(t), x(t - \tau_1(t)), \ldots, x(t - \tau_p(t))), \tag{1.4}$$

with $0 \leq \tau_j(t) \leq r; j = 1, 2, \ldots, p$,
Integro-Differential Equation (IDE)

$$\dot{x}(t) = \int_{-r}^{0} g(t, \theta, x(t + \theta) d\theta, \tag{1.5}$$

as well as State-Dependent Delay Differential Equation (SD-DDE)

$$\dot{x}(t) = f(x(t), x(t - h(x_t))), \tag{1.6}$$

where $f : \mathbb{R}^2 \to \mathbb{R}$ is known and $h : C((-r, 0], \mathbb{R}^n) \to [0, \infty)$ is a given functional. There are several well regarded books [70], [12], [43], [40], [3], [96] [158] [85] [57] [91] in the fields of pure and applied mathematics devoted to the qualitative theory of differential equations with delays. Although some of them might seem very theoretical without giving an outline of the possible applications in biology and ecology, they are essential sources and references for work on Functional Differential Equations (FDEs). Namely, the second version of the book by J.Hale (coauthored by S.V. Lunel) [70] covers the basic theory of FDEs and also takes into account most of the fundamental achievements in the field. This volume refers in particular to the basic existence theory, properties of the solution map, Liapunov stability theory, stability and boundedness in general linear systems, behavior near equilibrium and periodic orbits for autonomous retarded equations, global properties of delay equations and FDEs on manifolds, which makes a great reference for studies related to FDEs.

In addition to above mentioned developments of FDEs, various approaches have been applied in the study of FDEs. For instance, the fundamental principles underlying the interrelations between c^*-algebra and functional differential objects have been revealed in the book by A. Antonevich [12], where solvability conditions of various FDEs are investigated. In addition, the properties of solutions of FDEs have been examined with respect to oscillation theory in several study cases [57], [40], [3], [2] in which oscillatory and nonoscillatory properties of first, second and higher-order delay and neutral delay differential equations are addressed.

While there are several contributions regarding existence and uniqueness of solutions as well as solvability of FDEs, a foremost concern of many applied mathematicians is the behavior of the solutions of FDEs. Along with the new methods proposed in the study of FDEs, some major tools such as the method of characteristics or the method of Liapunov functionals employed in global and local analysis of ODEs and PDEs have been extended to the analysis of FDEs. These have been implemented in a vast number of studies concentrated on various mathematical models with delay. In particular, DDEs have been a great source for investigating the population dynamics of single or interacting species.
The history of DDEs applied in population biology goes back to predator-prey systems introduced by Italian mathematician Vito Volterra. In the 1920s he was asked to study the fluctuation observed in the fish population of the Adriatic Sea. In 1926 Volterra [180] constructed an interesting model of fish population (see the equation (1.9)). Around the same time, the chemist A.J. Lotka, proposed a similar model but in a distinct context [109], which would later be recognized as the Lotka-Volterra model. They established their original works on the expression of predator-prey relation in the form of nonlinear differential equations.

As delay models gained broader use in the second half of the twentieth century, the logistic equation was one of the first equations that was generalized with respect to time delay. The logistic growth model with discrete delay is due to the efforts of

Hutchison in 1948 [77]

$$\frac{du(t)}{dt} = \gamma u(t)\left[1 - \frac{u(t-\tau)}{k}\right], \tag{1.7}$$

in which $\tau \geq 0$ represents a discrete delay.
Slightly modified forms of equation (1.7) have been used in different experimental studies such as the population of sheep-blowfly [132], [66], [133], [112].

On the basis of the model (1.7), a local bifurcation analysis can be carried out by perturbation methods (i.e. let $\tau = \tau_0 + \epsilon$ with $0 < \epsilon \ll 1$ and substitute into the characteristic equation). This is used to demonstrate that small perturbations to the bifurcation value τ_0 may destabilize the nonzero steady state of (1.7) and periodic solutions may bifurcate from the steady state. Specifically, the period of unstable solutions of (1.7) can be determined and the existence of nonlinear solutions near the perturbed bifurcation value can be established through the procedure of "multiple-scales" (see for example [124]). The article by Mackey and Milto [116] and also [54] provides a good review of such analysis applied to the study of periodic dynamic diseases. To illustrate the bifurcating solutions of (1.7), let us consider the work of Tavernini [170] which uses the model (1.7) to study population dynamics of lemmings [169]. Let $\gamma = 3.5$ and $k = 19$; Then different situations arise when the delay $\tau > 0$ increases. Here, we use the Matlab DDE solver "dde23" to study the effects of delay on dynamics of the model. Figure 1.1 represents the phase-plane (i.e. the plane of (u, u'))of the model (1.7) near the nonzero steady state. As delay τ increased, oscillatory solutions bifurcate from the nonzero steady states. When delay passes through a critical value $\tau \approx 0.54$ periodic solutions bifurcate. Further increases to delay τ result in a global bifurcation. Namely, the system exhibits a homoclinic orbit for $\tau = 0.9398$. The orbit vanishes for larger values of τ and the solution may blow up. Figure 1.2 shows how the solutions of (1.7) evolve in time. The top Figure indicates the loss of stability of the nonzero steady state due to increases of delay. The middle Figure represents a delay induced periodic bifurcating solution. The bottom Figure indicates the pulse shape of the solution due to existence of the homoclinc orbit.

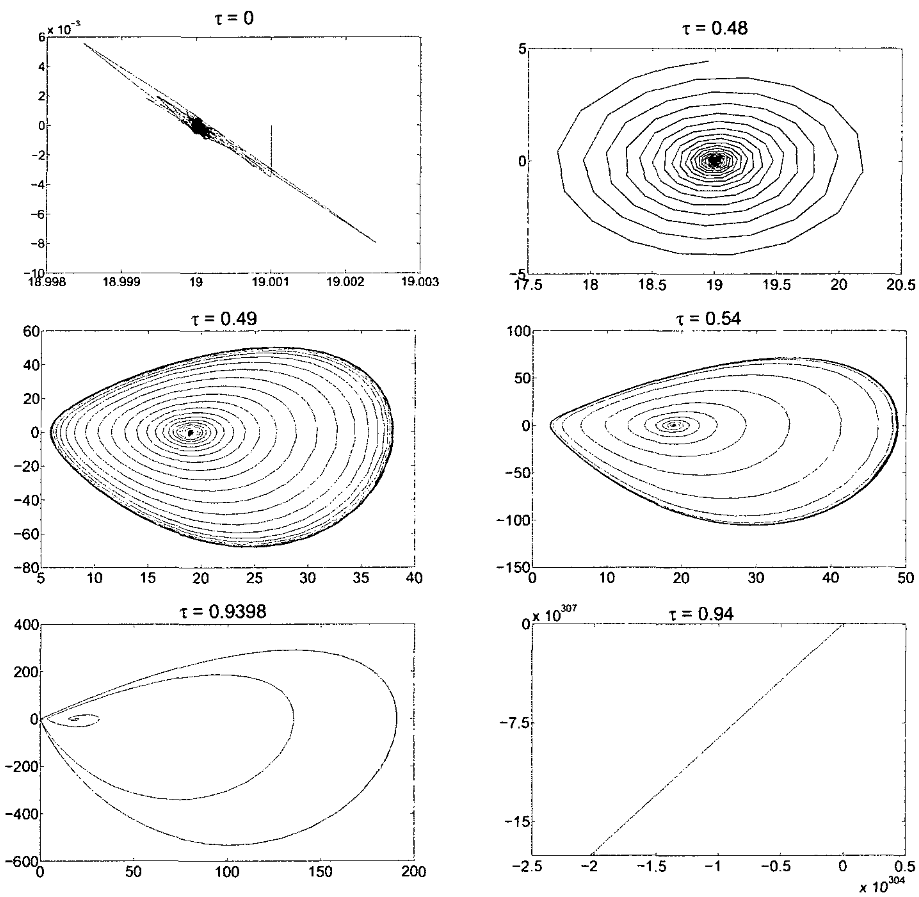


Figure 1.1: As delay τ increases, the periodic solution bifurcates from the nonzero steady state due to increases of delay. Figures are representing snapshots of the phase-plane (u, u') corresponding to the logistic equation (1.7) with $\gamma = 3.5$ and $k = 19$.

When the past dependence is through the derivative of the state variable, the equation is called a Neutral Functional Differential Equation (NFDE). Then the Hutchison's growth model (1.7) is extended to the following neutral delay logistic

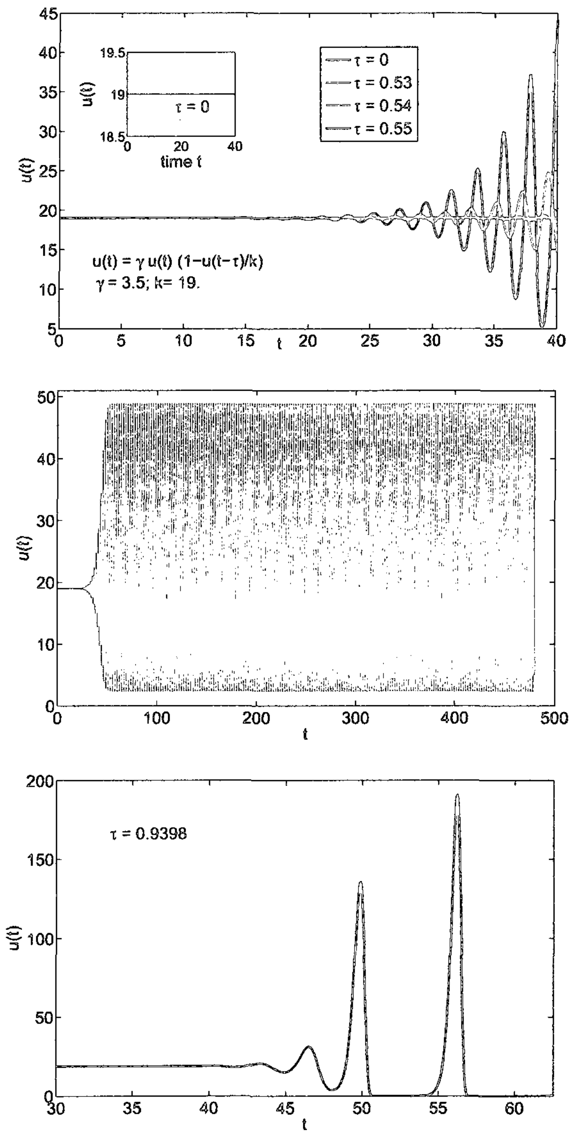


Figure 1.2: Model (1.7) describes the temporal behaviors of the population of Lemmings [170] Top: effect of delay on the nonzero steady state. The amplitude of oscillations increases when delay is increased. Middle: periodic solutions due to delay induced Hopf bifurcation; $\tau = 0.54$. Bottom: homoclinc solution emerges when delay is increased to a critical value $\tau = 0.9398$.

equation,

$$\dot{x}(t) = rx(t)\left[1 - (x(t-\tau) + \rho\dot{x}(t-\tau))/k\right], \tag{1.8}$$

which was first introduced by Gopalsamy and Zhang [58] in 1988. The global and local qualitative analysis of equation (1.8) and also the boundedness of its solutions have been investigated in distinct studies [50], [94], [51]. Based on equation (1.8), the neutral predator-prey and neutral competition models were introduced and studied by Kuang [92], [93].

Another extension to (1.7) is given by

$$\frac{du(t)}{dt} = \gamma u(t)\left(1 - \frac{u(t)}{k} - \frac{1}{Q}\int_p^t f(t-s)u(s)d(s)\right), \tag{1.9}$$

in which delay is incorporated into the integral term. Here γ, k and Q are positive, and instantaneous self-crowding term $f(t)$ is accompanied by a population term $u(t)$. Note that the population $u(t)$ rises to a maximum and then exhibits an exponential decay. Equation (1.9) is originally taken from Volterra's model for the effect of a deteriorating environment caused by the accumulation of waste products on mortality. In contrast with the commonly used equation (1.7) with discrete delay, equation(1.9) includes a type of delay that is known as distributed delay; which can be considered as the sum of infinitely numerous small delays in the form of an integral. There are certain assumptions made about the kernel $f(t)$ that will be discussed in the following chapters. Although discrete delay can be appropriate in various situations [61] [52], [53], [190], the use of distributed delay allows us to include stochastic effects in a model [37], [114]. Otherwise the model is considered to be deterministic.

When $Q = 1$ and $p = 0$ the integro-differential equation (1.9) can be used to model population growth of a parasite. This is presented in the work of MacDonald [114] in 1978.

Several delay models have been constructed to study the dynamics of infectious diseases such as Rabies, HIV, tuberculosis and influenza. In fact, a discrete delay can be added to the model to account for the time lag between the moment a cell gets infected and the point when infected cells start producing virus. Such a delay is considered in some recent works [121], [122], [130], [131], [140], [141], [73] which contribute toward correctly modeling the HIV infection process.

Including the spatial spread of population into delay systems has been one of the challenges in realistically modeling the multi-species, single-species and interacting-species populations which will be discussed in the next section and more explicitly in Section 1.3.

1.2 Waveforms in Biology and Ecology

A key element in a vast number of phenomena in biology and ecology is the appearance of a traveling wave in the spatial domain due to diffusion effects. Waves of chemical concentrations, spread of pest outbreak, colonization of space by a population, spatial spread of epidemics, traveling waves in predator-prey systems, waves in excitable media, traveling wavefronts of a growing population and multispecies population dynamics with dispersal are all examples of the abundant studies that have been conducted in the area of biological waves. Several introductory and advanced books have included a large number of mathematical models that are related to different wave phenomena in biology (see for example [125],[126], [187], [151], [28], [62], [135], [179], [189]).

Systems of Reaction-Diffusion (RD) equations have been the main source of modeling in study of various aspects of traveling wave behavior for decades. Although it has been recognized that some well-known results of traveling waves can be extended to delayed RD equations, in most of the cases, such extensions become highly non-trivial. In particular, the equations describing waves are no longer systems of ODEs but rather DDEs. Yet, there has been substantial progress in the study of traveling waves in delay RD systems (see for example [139], [149], [192], [165]). For now we concentrate on ordinary RD equations (i.e. RD systems with no delay term). Later we extend our discussion to delay RD equations.

A traveling wave is usually taken to be a wave which travels without change of shape. To describe traveling waves mathematically, consider the following ordinary RD system

$$\frac{du}{dt} = D\frac{\partial^2 u}{\partial x^2} + f(u), \tag{1.10}$$

where the vector $u(x,t) \in \mathbb{R}^n$ is for instance, the vector of different chemical concentrations at time t and space $x \in \mathbb{R}^m$, $f(u)$ represents kinetics and D is the diagonal matrix of diffusion coefficients. Then a solution $u(x,t)$ of (1.10) is a traveling wave if it is in the form of

$$u(x,t) = U(\nu \cdot x - ct) = U(z), z = \nu x - ct, \text{ with } x \in \mathbb{R}^m \text{ and } t > 0, \tag{1.11}$$

where ν is a unit vector in $\mathbb{R}^m$, c is a constant that is called speed of propagation and the dependent variable z is called the wave variable. Then $u(x,t)$ is a traveling wave moving at constant speed c in the direction ν without changing its shape. To be physically realistic, $u(z)$ must be bounded and nonnegative for all z. When $c = 0$, the wave becomes stationary and does not travel in any direction of the spatial domain.

Figure 1.3 represents typical shapes of traveling and stationary waves that are observed in different studies. A wave solution is periodic if we have $U(z+L) = U(z)$ for all z and for some $L > 0$. Front, back and pulse are wave solutions that are asymptotically constant. In particular, they converge to homogeneous steady states E_1 and E_2 of (1.10). For fronts (and backs) we have $E_1 < E_2$ ($E_1 > E_2$), $\lim_{z\to-\infty} U(z) = E_1$ and $\lim_{z\to+\infty} U(z) = E_2$, whereas pluses occur when $E = E_1 = E_2$ and $\lim_{z\to\pm\infty} U(z) = E$.

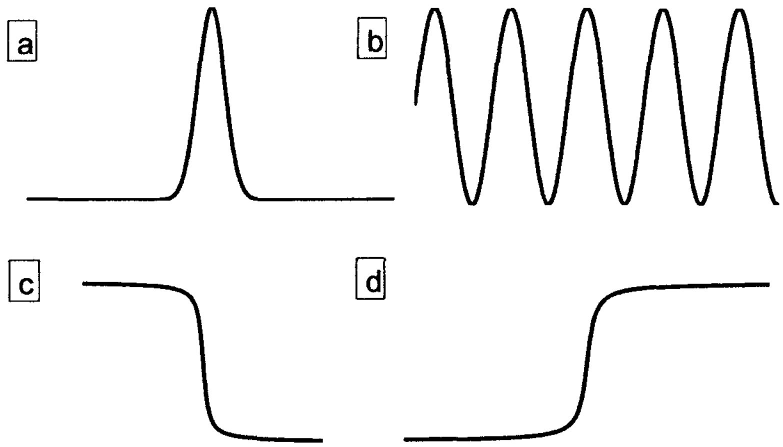


Figure 1.3: Typical wave solutions of RD systems: (a) wave pulse (b) periodic wave (c) waveback (d) wavefront

Note that wavefronts and backs are qualitatively similar and general outcomes are satisfied for both of them. In addition to vast applications of traveling wavefronts in biology, various kinds of waves have been observed in chemical reactions ([81], [179], [17] and references herein) as well as nonlinear optics [5], water waves [38], [39], [79], gas dynamics [160] and solid mechanics [171], [172], [173], [47]. Our primary concern in the present work is traveling and stationary wave solutions of the forms mentioned above.

In order to obtain solutions of the form (1.11), substitute $U(z)$ into (1.10). Then we have:

$$DU'' + cU' + f(U) = 0, \tag{1.12}$$

where $'$ denotes the derivative with respect to z.

Depending on the form of the reaction term $f(U)$ and also the initial condition $u(x,0) = u_0(x)$ on (1.12), a wave solution may or may not exist. For instance, when (1.10) is scalar and $f(U) = 0$, the solution of (1.12) is given by $U(z) = A + Be^{-\frac{cz}{d}}$

with A and B constant integration. Then by boundedness of $U(z)$, B must be zero and hence $U(z) = A$ which is not a traveling wave, but is just a constant solution. Moreover, depending on f there is a minimum c^* for the wave speed c. For values of c less than the minimal speed c^*, the wave solution may lose its monotonicity and become physically unrealistic (i.e. $U(z) < 0$ for some values of $z \in \mathbb{R}$). Moreover, the minimal speed c^* is often considered to be greater than zero and the case $c = 0$ describes stationary waves that do not move at all. Generally speaking, the wave speed is dependent on the form of reaction terms in RD equations [155]. As we will show later, in simple cases, wave speed can be presented in terms of parameters associated with the reaction term $f(u)$ and the diffusion matrix D.

In order to have a better understanding of traveling wave solutions of ordinary RD equations, consider the following two examples.

1a. Fisher-Kolmogoroff RD equation

Consider the following nonlinear ordinary RD equation which was first proposed by Fisher [49] to study the spatial spread of a favored gene in a population

$$\frac{du}{dt} = \frac{\partial^2 u}{\partial x^2} + u(1-u). \tag{1.13}$$

In the same year, this equation and its traveling wave solution was studied in the work by Kolmogoroff et al. in 1937 [89]. In order to demonstrate traveling wave solutions of the scalar one-dimensional Fisher-Kolmogoroff equation (1.13), consider

$$u(x,t) = w(x-ct) = w(s), s = x - ct. \tag{1.14}$$

Then we arrive to the wave profile equation

$$w'' + cw'(s) + w(1-w) = 0. \tag{1.15}$$

Since (1.13) is invariant if $x \to -x$, c can be considered positive or negative. Here, without loss of generality we assume that $c \geq 0$.

While equation (1.13) has been a basis for a large number of different models such as spread of early farming in Europe [9], [10], gene culture and waves of advance [11], it has also received continuous attention in the search for analytical wave solutions [89], [23], [95], [157], [68], [80], [48], [88]. Yet, there is no general analytic solution available for either equation (1.13) or (1.15). Nevertheless, diverse methods can be applied to find an approximation of the solution of (1.13) (see for example [147], [147]). For the wave profile equation (1.15), there is an exact solution for a particular c greater than 2 (see [125] Chapter 13). Moreover, the asymptotic solutions of (1.15) for the case $0 < \frac{1}{c^2} \ll 1$, can be obtained [124], [84], [31] by multiple scale and singular perturbation methods. Monotone iteration methods can also be used to construct an iterative wave solution of a generalized form of (1.15) with discrete delay [189]. The two steady states of (1.13) are $E_1 = 0$ and $E_2 = 1$, where the wave solution $w(s)$ connects E_1 and E_2 as s tends to $+\infty$ and $-\infty$ respectively.

It can be easily verified that E_2 is a saddle and for $c > 2$, E_1 is a stable node. Also $c < 2$ causes E_1 to be a stable spiral. Since a spiral steady state results in oscillatory behavior of the wave solution, it is important to consider a minimal speed $c^* = 2$. Specifically, by continuity arguments, there is a trajectory from E_2 to E_1 lying in the second quadrant (i.e. $w \geq 0$ and $w' \leq 0$) of the phase-plane, with $0 \leq w \leq 1$ for all wave speeds $c \geq c^* = 2$. For $c < 2$ there are trajectories connecting the unstable saddle E_2 to the stable spiral at origin (i.e. E_1) and hence they spiral around the origin as $z \longrightarrow -\infty$. Therefore, in this case the traveling waves take negative values which is physically and biologically unrealistic.

Although traveling waves are usually described as solutions of the form (1.11), the following example represents a case in which the wave can travel in all directions of the spatial domain. Waves of this type are known as target waves or target patterns.

2a. A linear RD model for biological invasions

Let $f(u) = \alpha u$ with $\alpha > 0$ in equation (1.10); then we have a linear RD equation which is a simple population model of exponential growth (i.e. Malthusian populations) with diffusion that is used for biological invasions such as muskrat dispersal in Europe [156], invasion of the nine-banded armadillo in the United States [76] and spread of larch casebearer in northern Idaho [108]. Fortunately, the Cauchy problem corresponding to the linear model can be solved analytically. In particular consider

$$\begin{cases} \frac{\partial u}{\partial t} &= D\frac{\partial^2 u}{\partial x^2} + \alpha u, \text{ with } \alpha > 0 \text{ and } x \in \mathbb{R}, \\ u(x,0) &= M\delta(x), \end{cases} \tag{1.16}$$

where $\delta(x)$ is the Dirac delta function. In an ecological context, this corresponds to a case that a population u is initially concentrated at origin $x = 0$ and diffuses in an unbounded space. While the method of separation of variables and method of Fourier transform [90] are applicable to the problem (1.16), we take an alternative approach. Let $h(x,t)$ be the solution of the heat equation (i.e. equation (1.16) with $\alpha = 0$); then it can be easily shown that the solution $u(x,t)$ of (1.16) takes the form

$$u(x,t) = f(t)h(x,t), \tag{1.17}$$

where $f(t)$ is the solution of

$$\frac{df}{dt} = \alpha f. \tag{1.18}$$

Hence, $u(x,t) = e^{\alpha t}h(x,t)$. Using the method of similarity of variables [143], the heat equation

$$\frac{\partial h}{\partial t} = D\frac{\partial^2 h}{\partial^2 x}, \tag{1.19}$$

can be solved as follows.

Set $h(x,t) = \phi(\lambda(x,t))$, where $\lambda(x,t) = \frac{x}{2\sqrt{Dt}}$. Then $h(x,t)$ is a solution of (1.19) if and only if $\phi(x)$ is a solution of

$$\phi'' + 2\lambda\phi' = 0. \tag{1.20}$$

Integrating the ODE (1.20), we get that

$$h(x,t) = erf\left(\frac{x}{2\sqrt{Dt}}\right), \tag{1.21}$$

where $erf(s)$ is the error function defined by

$$erf(s) := \frac{2}{\sqrt{\pi D}}\int_0^s e^{-r^2}dr. \tag{1.22}$$

Differentiating (1.22) and evaluating $s = \frac{x}{2\sqrt{t}}$, we get that the heat kernel is given by

$$k(x,t) = \frac{1}{2(\pi Dt)^{\frac{1}{2}}}\exp\left(-\frac{x^2}{4Dt}\right); \tag{1.23}$$

See [143] for more details. Hence the solution of the Cauchy problem (1.16) is uniquely determined by

$$u(x,t) = M\int_{-\infty}^{\infty} k(x-y,t)e^{\alpha t}\delta(y)dy.$$

Using the properties of the Dirac delta function $\delta(x)$, the solution of (1.16) is given by

$$u(x,t) = \frac{M}{2(\pi Dt)^{\frac{1}{2}}}\exp\left\{\alpha t - \frac{x^2}{4Dt}\right\}. \tag{1.24}$$

In order to see how a wave solution travels with time, let $u = k = constant$ (i.e. consider a front of isoconcentration of the population). Then solve (1.24) with respect to x/t [83]. This gives the result:

$$x/t = \pm\left[4\alpha D - 2Dt^{-1}\ln t - 4Dt^{-1}\ln((2\pi D)^{\frac{1}{2}}k/M)\right]^{\frac{1}{2}}. \tag{1.25}$$

Then the asymptotic solution (i.e. as $t \to \infty$) of $u(x,t) = k$ is given by,

$$x/t = \pm 2(\alpha D)^{\frac{1}{2}} = c. \tag{1.26}$$

In other words the population wavefront propagates outward from the initial disturbance at the origin with a speed ultimately equal to $2(\alpha D)^{\frac{1}{2}}$.

Further studies on the general solutions of (1.16) with the following Gaussian initial distribution

$$u(x,0) = \frac{M}{(2\pi)^{\frac{1}{2}}\sigma} \exp(-x^2/2\sigma_0^2), \tag{1.27}$$

where σ_0^2 is the variance, indicate the same speed of propagation, $2(\alpha D)^{\frac{1}{2}}$ [32].

One might conclude that the same would be true for any initial condition, but it is only true if the amplitude of the initial condition has a sufficient rapidity as $|x|$ tends to infinity [83]; [123]; [129].

Extension of the procedure to unbounded two-dimensional spatial domains is fairly straightforward. Then the solution of the Cauchy problem

$$\begin{cases} \frac{\partial u}{\partial t} &= D(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2}) + \alpha u, \text{ with } \alpha > 0 \text{ and } (x, y) \in \mathbb{R}^2, \\ u(x, y, 0) &= M\delta(x)\delta(y), \end{cases} \tag{1.28}$$

is given by

$$u(x, y, t) = \frac{M}{2(\pi D t)^{\frac{1}{2}}} \exp\left\{\alpha t - \frac{x^2 + y^2}{4Dt}\right\}. \tag{1.29}$$

Solutions of this type are known as target patterns (see for example [55], [86]). Here, the circular shaped waves propagate from the origin. Specifically, Figure 1.4 represents the solutions of the Cauchy problems with respect to one and two-dimensional spatial domains for $\alpha = 0.3, D = 100$ and $M = 200$. Note that the amplitude of the target waves decreases until the solution reaches its local minimum with respect to t, then the amplitude increases in the entire domain. In an ecological sense, this type of behavior can be understood as formation of new colonies due to overcrowding. Namely, the population is initially overcrowded at the origin. Then individuals must choose new colonies at a distance relatively close to the origin. This decreases the amplitude of population density while individuals spread into the spatial domain. As time evolves the population of each colony increases and therefore the amplitude of the population density grows with respect to the origin.

Although the linear relation (i.e. $f(u) = \alpha u$) in (1.16) sounds realistic for many models in biology and ecology, the essential role of nonlinearity is crucial in a large

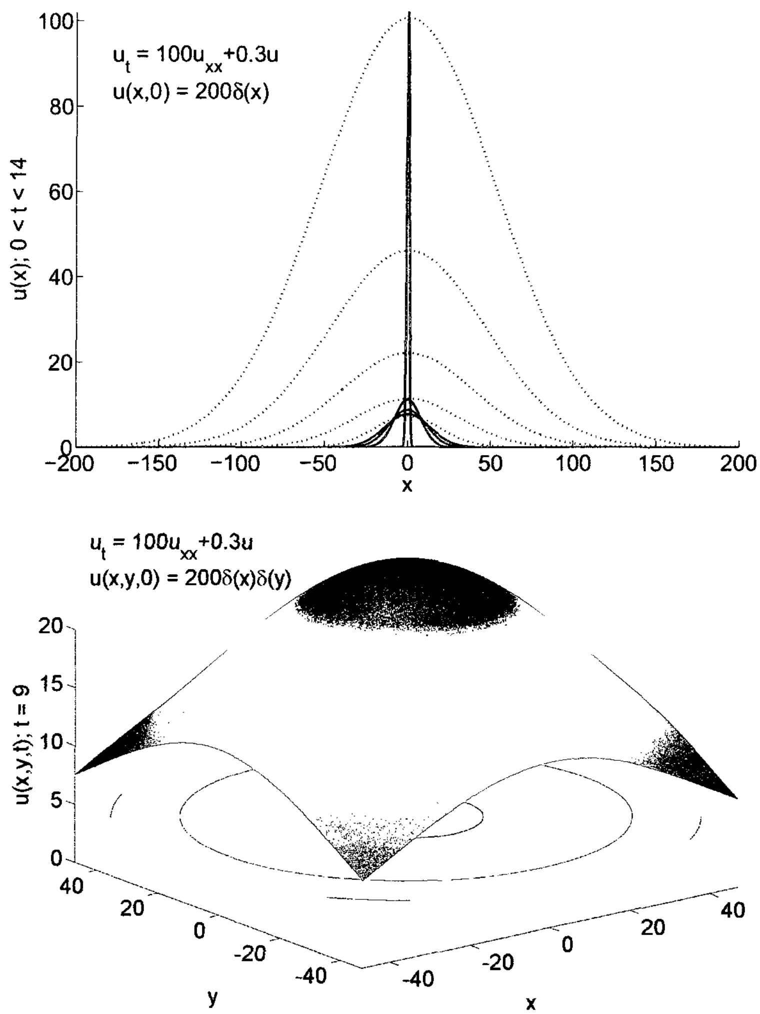


Figure 1.4: Top: the amplitude of the target waves decreases (shown with solid lines) until the solution reaches its local minimum with respect to t, then the amplitude increases (shown with dashed lines) in the spatial domain. Bottom: the traveling target waves in two-dimensional space.

variety of models. In fact, several researchers have developed RD models that can provide better descriptions of more complicated problems (see for example [100], [153], [152],[101], [127]).

Several studies include traveling wave solutions of delayed RD equations without nonlocal effects. Namely, the existence, uniqueness and asymptotic behavior of the wave solutions corresponding to the delayed RD equation,

$$\frac{\partial u(x,t)}{\partial t} = \frac{\partial^2 u(x,t)}{\partial x^2} + f(u(x,t), u(x,t-\tau)), \tag{1.30}$$

with $0 \leq u(x,t) \leq 1$ for $x \in \mathbb{R}$, $t > 0$ have been explicitly studied in the book by Wu [189]. In particular, the method of phase-plane (i.e. implementation of graph equation for trajectories), linearization, comparison of trajectories and their continuous dependence on wave speed c, method of super- and subsolutions combined with some results already known from ODEs have been used to show existence and uniqueness of minimal speed c^*_τ and a nontrivial strictly increasing wave solution corresponding to (1.30). Furthermore, an iteration scheme in conjunction with the fixed point theorem can be used to construct traveling waves in a system of RD equations of the form (1.30).

The methods mentioned above are some common methods employed to study traveling wave solutions of RD systems with discrete or distributed delay. In the present work we will employ some of these methods along with other applicable methods that will be discussed in the upcoming sections. In the following we study the effect of delay on the wave solutions of the previous two examples.

1b. Delayed Fisher-Kolmogoroff RD equation

Let $f = u(x,t-\tau)[1-u(x,t)]$ in the equation (1.30), then we have

$$\frac{\partial u(x,t)}{\partial t} = \frac{\partial^2 u(x,t)}{\partial x^2} + u(x,t-\tau)[1-u(x,t)], \tag{1.31}$$

which is the natural extension of the logistic growth population model (1.7) and the original Fisher-Kolmogoroff RD equation. Here the population disperses via linear diffusion and the time delay $\tau > 0$ represents the time required for the food supply (of the population) to recover from grazing (i.e. food supply at time t depends on population size u at time $t - \tau$).

The two steady states of (1.31) are $E_1 = 0$ and $E_2 = 1$ where E_1 is dependent on τ. Using the following linear transformation we can obtain a delay independent steady state E_1,

$$\widetilde{u} = \begin{cases} \frac{u-E_1}{E_2-E_1} \text{ if } E_1 \neq E_2 \\ u - E_1 \text{ otherwise.} \end{cases} \tag{1.32}$$

For technical reasons, let $s = x + ct$ in (1.14). Then the wave profile equation corresponding to (1.31),

$$w''(s) - cw'(s) + w(s - c\tau)[1 - w(s)] = 0, \tag{1.33}$$

can be linearized around the new delay independent steady states E_1 and E_2 resulting in characteristic functions

$$\Lambda_\tau^{E_i}(\lambda) := \lambda^2 - c\lambda + \alpha + \beta e^{-\lambda c\tau}, \tag{1.34}$$

where α and β are correspondingly the partial derivatives of $w(s - c\tau)[1 - w(s)]$ with respect to $w(s)$ and $w(s - c\tau)$ evaluated at E_i. Similar to the case with no delay, the minimal speed c_τ^* the minimal speed is defined as the infimum of c such that the characteristic equation (1.34) for E_1 has at least one real root. Namely,

$$c_\tau^* := \inf\left\{\, c > 0; \text{ there is } s \in \mathbb{R} \text{ with } \Lambda_\tau^{E_1}(s) = 0\right\}. \tag{1.35}$$

In fact, it can be shown that $c_\tau^* > 0$ and for all $c > c_\tau^*$, there are exactly two real roots of $\Lambda_\tau^{E_1}$ such that $0 < \lambda^-(c) < \lambda^+(c) < c$. Moreover, for $c = c_\tau^*$ there is exactly one real root $\lambda^* \in (0, c^*)$ [189].

Since we let $s = x + ct$ and therefore the wave solution moves in the negative x-direction. The steady state E_1 is an unstable stable node. In particular, it can be shown that for all $c > c^*$ there exists a unique (up-to-translation) nontrivial wave solution of (1.33) with asymptotic behavior,

$$w_c(s) = ke^{\lambda^-(c)s}[1 + O(1)] \text{ as } s \to -\infty, \tag{1.36}$$

where k is a constant.[189].

To show the effects of delay on the behavior of the traveling wave solution of (1.33), we have used the Matlab DDE solver, dde23 for $\tau > 0$ and the ODE solver ode45 for the case that $\tau = 0$. Figure 1.5 represents the traveling wave solutions of (1.33). Observe that as delay τ increases from zero to positive values, the wave starts to oscillate from E_2. This is due to the fact that c^*_τ is an increasing function of τ (see [139] for more details). Hence, as delay is increased, the wave speed $c = 2$ becomes less than the minimal speed c^*_τ and causing oscillations of the wave solutions.

2b. Delayed linear RD models

The linear model (1.16) can be generalized in diverse ways. In order to show the effect of delay on spatio-temporal behavior of the population density $u(x,t)$, consider the following Cauchy problem,

$$\begin{aligned} \frac{\partial u(x,t)}{\partial t} &= D\frac{\partial^2 u(x,t)}{\partial x^2} + \alpha u(x, t-\tau), t > 0, x \in \mathbb{R}, && (1.37) \\ u(t,x) &= Mf(x) \text{ for } \ t \in [-\tau, 0], && (1.38) \end{aligned}$$

where $f(x)$ decays at $x = \pm\infty$ and M is a constant.

Let $u(t,x) = X(x)T(t)$. Using the method of separation of variables, equation (1.37)

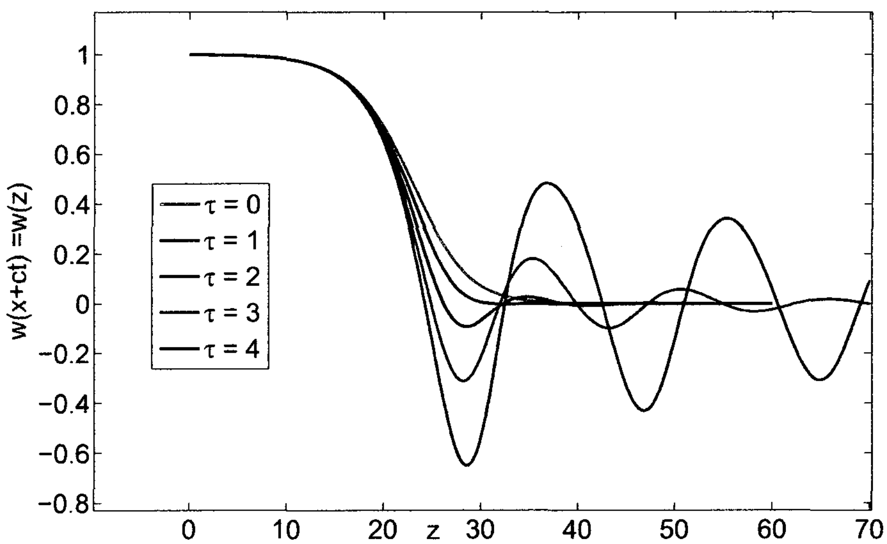


Figure 1.5: By increasing τ the stability of E_1 and also monotonicity of the wavefront are lost. The plots represent the effect of delay on Fisher-Kolmogoroff traveling wavefronts for c=3 and initial history function 0.99.

is reduced to ODEs

$$x''(x) - \lambda X(x) = 0, \tag{1.39}$$

$$T'(t) - \lambda D T(t) - \alpha T(t-\tau) = 0. \tag{1.40}$$

Equation (1.40) is a first order linear ODE that can be solved with the Lambert W function. In particular, the solution is in the form of

$$T(t) = e^{vt}, \tag{1.41}$$

where v is the root of the characteristic equation

$$v - \lambda D - \alpha e^{v\tau} = 0. \tag{1.42}$$

Note that since equation (1.42) has infinitely many roots, the solution (1.41) is not unique. A root of (1.42) is found by the Lambert W function which is the inverse of the function $f(\theta) = \theta e^{\theta}$. In particular, let $z = v - \lambda D$, then equation (1.42) is rewritten

$$z = \alpha e^{-(z+\lambda D)\tau}. \tag{1.43}$$

This is equivalent to

$$tze^{zt} = \tau\alpha e^{-\lambda D t}. \tag{1.44}$$

Hence,

$$z = \tau^{-1} W(\tau\alpha e^{-\lambda D t}), \tag{1.45}$$

and we get that

$$v = \tau^{-1} W(\tau\alpha e^{-\lambda D t}) + \lambda D. \tag{1.46}$$

By the entropy principle [64], $T(t)$ must decay as t increases. Therefore, we must assume that $\lambda < 0$. Let $\lambda = -\omega^2$. Then solving (1.39), we get that

$$X(x;\omega) = C_1(\omega)e^{i\omega x} + C_2(\omega)e^{-i\omega x}. \tag{1.47}$$

Also considering dependence of v to ω, solution (1.41) is rewritten

$$T(t;\omega) = e^{v(\omega)t}. \tag{1.48}$$

Hence the general solution of (1.37) is

$$\begin{aligned} u(x,t) &= \textstyle\int_0^\infty X(x:\omega)T(t;\omega)d\omega, \\ &= \textstyle\int_0^\infty C_1(\omega)e^{v(\omega)t+i\omega x}d\omega + \int_0^\infty C_2(\omega)e^{v(\omega)t-i\omega x}d\omega. \end{aligned} \tag{1.49}$$

By changing the variable ω in the second integral to $-\omega$, we get that

$$\begin{aligned} u(x,t) &= \textstyle\int_0^\infty C_1(\omega)e^{v(\omega)t+i\omega x}d\omega - \int_0^{-\infty} C_2(-\omega)e^{v(\omega)t+i\omega x}d\omega, \\ &= \textstyle\frac{1}{\sqrt{2\pi}}\int_{-\infty}^\infty \hat{f}(\omega)e^{v(\omega)t+i\omega x}d\omega, \end{aligned} \tag{1.50}$$

where

$$\hat{f}(\omega) = \begin{cases} \sqrt{2\pi}C_1(\omega) & \text{for } \omega > 0, \\ \sqrt{2\pi}C_2(-\omega) & \text{for } \omega < 0. \end{cases} \tag{1.51}$$

In fact, $\hat{f}(\omega)$ is the Fourier transform of the initial history function (1.38). Thus

$$\hat{f}(\omega) = \frac{M}{\sqrt{2\pi}}\int_{-\infty}^{\infty} f(x)e^{-i\omega x}. \tag{1.52}$$

Changing the variable x to y and substituting (1.52) into (1.50) yields

$$u(x,t) = \frac{M}{2\pi}\int_{-\infty}^{\infty}\left[\int_{-\infty}^{\infty} f(y)e^{-i\omega y}dy\right]e^{v(\omega)t+i\omega x}d\omega. \tag{1.53}$$

Using the Fubini's Theorem [175], the order of integral can be changed and we have

$$u(x,t) = \frac{M}{2\pi}\int_{-\infty}^{\infty} f(y)\left[\int_{-\infty}^{\infty} e^{v(\omega)t+i\omega(x-y)}d\omega\right]dy. \tag{1.54}$$

Hence the Cauchy problem (1.37)-(1.38) is reduced to the problem of evaluating the inner integral in the solution (1.54).

Another extension to the model (1.16) is when a distributed delay is taken into account. Specifically, the delay model takes the form

$$\frac{\partial u(x,t)}{\partial t} = D\frac{\partial^2 u(x,t)}{\partial x^2} + \alpha\int_{-\infty}^{t} K(t-\theta)G(u(x,\theta))d\theta, \tag{1.55}$$

where K and G are continuous functions.

Let the solution $u(t,x)$ be separable with respect to space and time; then the corresponding temporal equation can be reduced to a system of ODEs if and only if the function $K(\theta)$ is a linear combination of the form

$$K(\theta) = \sum_{m=1}^{n} a_m t^{m-1} e^{\ell\theta}, \tag{1.56}$$

where ℓ, m and $n \geq 1$ are constants.

The reduction to ODEs is based on the method of the linear chain trick which was introduced by Fargue [46] in 1973. The method is broadly used in various studies (see for example [188], [115], [144]). In order to demonstrate the procedure of finding the analytic solution, let $K(\theta) = e^{-\theta}$. Consider the following Cauchy problem corresponding to delay model (1.55),

$$\frac{\partial u(x,t)}{\partial t} = D\frac{\partial^2 u(x,t)}{\partial x^2} + \alpha \int_{-\infty}^{0} e^{\tau} u(x, t+\tau) d\tau, \tag{1.57}$$

$$u(x,t) = Mf(x) \text{ for } t \in (-\infty, 0]. \tag{1.58}$$

Let $u(x,t) = X(t)T(t)$; then similar to the previous case, equation (1.57) is reduced to

$$X''(x) - \lambda X(x) = 0, \tag{1.59}$$

$$T'(t) - \lambda D T(t) - \alpha \int_{-\infty}^{0} e^{\tau} T(t+\tau) d\tau = 0. \tag{1.60}$$

Let

$$y(t) = \int_{-\infty}^{0} e^{\tau} T(t+\tau) d\tau. \tag{1.61}$$

Then equation (1.60) is reduced to the linear system of ODEs,

$$T'(t) = \lambda D T(t) + \alpha y(t), \tag{1.62}$$

$$y'(t) = T(t) - y(t). \tag{1.63}$$

By the fundamental theorem of linear systems [142], the solution of (1.62)-(1.63) is found

$$T(t) = d_1 e^{\beta_1 t} + d_2 e^{B_2 t}, \tag{1.64}$$

where

$$\beta_1 = \frac{(\lambda D - 1) + \sqrt{(\lambda D + 1)^2 + 4\alpha}}{2},$$
$$\beta_2 = \frac{(\lambda D - 1) - \sqrt{(\lambda D + 1)^2 + 4\alpha}}{2},$$

and d_1, d_2 are constants. Again by the entropy principle [64], $T(t)$ must be decreasing. Hence, it is required that

$$\lambda = -\omega^2, \tag{1.65}$$

where $\omega > \omega_0 = \sqrt{\frac{\lambda}{D}}$.
Then the solution (1.64) is rewritten

$$T(t;\omega) = d_1 e^{\beta_1(\omega)t} + d_2 e^{\beta_2(\omega)t}, \tag{1.66}$$

with $\omega > \omega_0$ Then similar to (1.49) the general solution of (1.57) is given by

$$u(x,t) = \int_{\omega_0}^{\infty} X(x;\omega)T(t;\omega)d\omega. \tag{1.67}$$

Following the same procedure outlined in (1.50)-(1.54) we have

$$u(x,t) = \frac{M}{2\pi}\int_{-\infty}^{\infty}\left[\int_{-\infty}^{\infty} T(t;\omega)e^{i(x-y)}d\omega \; - \int_{-\omega_0}^{\omega_0} T(t;\omega)e^{i(x-y)}d\omega\right]dy, \tag{1.68}$$

which is the problem of finding the inner integrals. This is certainly achievable if not explicitly then through the numerical methods. The next section deals with more complicated models and it provides discussion on recent approaches for mathematical modeling of population dynamics.

1.3 Nonlocality: Interweaving delay and diffusion

The purpose of this section is to present two major developments in modeling single-species populations. Briefly, Britton's approach [29], [30] takes into account the aggregation mechanism of the population through a spatio-temporal convolution while the Smith-Thieme approach [161] incorporates age structures into the population models.

Delay logistic models presented in equations (1.7) or (1.9) are suitable in cases where the population is spatially uniform. However, in most cases the population densities may vary in space. Spatial dispersal has been widely modeled and investigated in population dynamics. Nevertheless, the greater part of the existing literature deals with either spatially homogeneous population density or a naive case of spatial inhomogeneity in which motion of individuals is introduced to the model only by Fick's Law. That is to say generally, the population flux is proportional to the concentration gradient. The approach of population spread due to Fickian diffusion assumes that individuals move around in a random way. Therefore, the population spreads out as a result of irregular motion of individuals (see for example [125] Chapter 11, [135] Chapter 2). Then such a simplistic assumption translates into a partial differential equation just by adding a Laplacian term to the corresponding ODE or DDE model (such as (1.7) or (1.9)) to represent the diffusion in population dynamics. In particular, equation (1.7) is changed to a one-dimensional delayed RD equation,

$$\frac{\partial u(x,t)}{\partial t} = D\frac{\partial^2 u(x,t)}{\partial x^2} + \gamma u(x,t)\left[1 - \frac{u(x,(t-\tau))}{k}\right]. \tag{1.69}$$

Equations of this type have many defects in describing the behavior of systems where population densities are variant in space. This is due to failure of diffusion term to describe complex motions. For instance, there can be an advantage to individuals in the population to aggregate. Generally speaking, aggregation of individuals is due to many reasons such as defense against predation [135], social purposes or preying on larger species [71]; [145], [136]. Then the motion of individuals in many cases is not just random and unbiased Fickian diffusion may not be solely suitable for modeling aggregation mechanisms. Some authors have attempted to resolve issues of this type by introducing convective, nonlinear diffusion or advective terms [67], [120], [154], [29] which have moderately improved the situation. Nonetheless, one should note that projecting some dynamical behaviors of a population into a single deterministic diffusive model is a highly non-trivial task.

Detailed discussions of diffusion in an ecological context have been included in various studies [28], [97], [98], [99], [134], [135]. Yet, there have been several difficulties in capturing the spatial variation of population densities by only adding diffusion terms. Namely, in modeling and analysis of ecological systems involving both time delay and diffusion, it is necessary to consider an interaction between delay and diffusion. Otherwise, local aggregation is overlooked and the model is not realistic. N.F. Britton was the first to address this issue [29] and tried to resolve it by involving the delay term into a weighted spatial averaging over the whole infinite domain [30].

Later Gourley and Britton [59] developed the idea of considering the aggregation of individuals to their present position from all possible positions at previous times. They implemented such methodology by developing a delayed predator-prey system incorporating spatial averaging. Further developments on delayed models such as (1.7) were made by introducing spatial averaging on a finite spatial domain [60]. Moreover, spatial movement may involve time delays that give rise [184] to a system of NFDEs or a hyperbolic parabolic nonlocal functional differential equation [146], [138], [137]. Later Smith and Thieme [161] employed the method of integration along the characteristic of an age-structured population model to derive a system of DDE with two age classes (mature and immature) and spatial dispersal among discrete patches. Lattice delay differential equations (LDDEs) with global interaction [185] is an outcome of the novel extension of Smith-Thieme approach to the case of infinite number of discrete patches. This was later extended [166] to a continuous spatial environment.

The above-mentioned approaches in modeling delay and diffusion simultaneously are remarkable advances in the modeling and analysis of spatially variant delayed population dynamics. Both approaches lead to delayed nonlocal diffusive systems that are mathematically challenging. The next two parts are devoted to presenting these approaches in unbounded one-dimensional spatial domains.

Part I. Britton's approach: spatio-temporal convolution

In 1989 N.F. Britton [29], [30] utilized probabilistic and also random walk arguments to introduce local aggregation and global intraspecific competition into a model for a single biological population in an infinite spatial domain. He proposed a mechanism such that the individuals of the population are moving (by diffusion) so that the force of intraspecific competition depends on population levels in a neighborhood of the original position, that is to say, on a spatial average weighted according to distance from the original position. In other words, if competition is for a common resource, then for mobile animals the important factor is the depletion of that resource in their neighborhood. So population effects should depend on an average population density in that neighborhood. In addition, the lags in space and time should be respectively considered in the model due to the assumptions that animals take time to move and that the resources take time to recover once consumed. In particular, an individual that is at position x at time t may not have been at position x at any prior time $t-\tau$, but at some other position y. Thus, for the simplest possible model, the competitive pressure at y and $t-\tau$ is proportional to $u(y,t-\tau)$. We then need to sum over all possible previous positions. Then the competitive effect is modeled by

$$\lim \sum_{y} \sum_{\tau} P((y,t-\tau)|(x,t))u(y,t-\tau)w(\tau)\delta y\delta\tau, \tag{1.70}$$

as $\delta y \to 0$ and $\delta\tau \to 0$, where P is a conditional probability density function of the individual having been at y and $t-\tau$ if it is at x and t now; the function $w(t)$

represents the weight given at time t to previous times $t-\tau$ which is assumed to depend on τ only. Moreover w is a monotone decreasing function with $\lim w(\tau) = 0$ as $\tau \longrightarrow \infty$.

In this manner it is assumed that competition takes place if the random walks of members of the population coincide. Note that competition is considered to be pointwise in both space and time.The limit term justifies a spatio-temporal convolution that is included in the reaction term of the model. Namely, the well-known KPP or Fisher-Kolmogroff equation [49] (i.e. equation (1.13)) is extended to a delayed nonlocal reaction diffusion equation of the form

$$\frac{du(x,t)}{dt} = \frac{\partial^2 u(x,t)}{\partial x^2} + u(x,t)\left[1 + \alpha u(x,t) - (1+\alpha)(h * u)(x,t)\right], \tag{1.71}$$

where the convolution $h * u$ is defined by

$$(h * u)(x,t) = \int_{-\infty}^{t} \int_{-\infty}^{\infty} h(x-y, t-\tau) u(y,\tau) dy d\tau, \tag{1.72}$$

subject to the normalization condition $h * 1 = 1$.

The growth rate in (1.71) is given by $1 + \alpha u - (1+\alpha) h * u$ in which αu represents the promoting effect of local aggregation and $-(1+\alpha)h * u$ with $\alpha > -1$ represents a global delayed self-limiting mechanism that works due to depletion of food when the global population becomes too large.

Let individuals be moving randomly with diffusion coefficient normalized to unity; then by considering the heat kernel for P we have

$$P((y, t-\tau)|(x,t)) = \frac{1}{(4\pi t)^{n/2}} \exp\left(\frac{-|x-y|^2}{4\tau}\right), \tag{1.73}$$

where n is the dimension of space.

In other words, in the limit expression (1.70) P takes the form of

$$h(x,t) = \frac{1}{(4\pi t)^{n/2}} \exp\left(-\frac{|x|^2}{4t}\right) u(t), \tag{1.74}$$

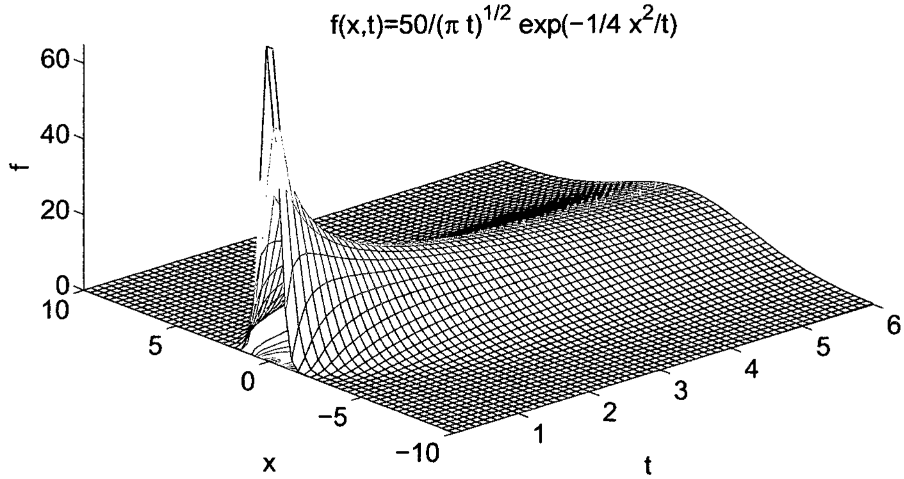


Figure 1.6: plot of the kernel $h(x,t)$ of spatio-temporal average $h * u(x,t)$ with $x \in [-10, 10]$ and $0 < t \leq 6$

where $h(x,t)$ is basically the heat kernel of the one-dimensional case. This has been presented in Figure 1.6.

Equation (1.71) can be extended to

$$u_t = u_{xx} + u(1 + \alpha u - \beta u^2 - (1 + \alpha - \beta)h * u), \tag{1.75}$$

with $0 < \beta < 1 + \alpha$, where $-\beta u^2$ represents a saturation term which mitigates against local crowding, when competition for space itself rather than resources becomes important. Employing the parabolic maximum principal, it can be shown that the solution of (1.75) cannot blow up. In addition, with appropriate initial and boundary conditions the solution cannot exceed the positive root of $1+\alpha u-\beta u^2 = 0$ (see [30] for more details).

The work by Britton [29] includes a nonlinear stability analysis for the uniform steady state solution $u \equiv 1$ of (1.71). Furthermore, standard bifurcation theory is applied to investigate periodic spatial structures in an infinite domain. Namely, Hopf bifurcations to a traveling wave solution and also to a standing wave solution have been demonstrated. However, the significance of Britton's work arises from his novel idea of including nonlocality in the form of spatio-temporal convolution into the reaction-diffusion (RD) equations describing a single or multiple species population dynamics. Although including spatio-temporal convolution into the population models may considerably complicate the analysis of the systems, it seems to be a necessary step forward in correctly modeling complex behaviors of members of a population.

Part II. Smith-Thieme approach: structured models

A major deficiency of many population models is that they do not take into account any age structure which may substantially influence the population size and growth. There are several books [87], [33], [113], [135] that give a good survey about age-structured models and their applicability. Namely, the book by H. Thieme [174] provides full detail of structured and unstructured population models. To see how different structures are taken into account, consider a population of a single species which is distributed over a habitat. Moreover, assume the habitat is not homogeneous and is divided into finitely many, let us say two, subhabitats (patches), each of which offers a different quality of life. Then in a simplified form [113], using the approach of Smith and Thieme [161], the above-mentioned situation is modeled by giving different per capita death rates $d_i(a)$ at age a for each patch i and different species dispersal $D_j(a)u_j(t,a)$ at age a from patch j to patch i where $i \neq j$. Accordingly, the structured model is presented by

$$\begin{cases} \frac{\partial u_1(t,a)}{\partial t} + \frac{\partial u_1(t,a)}{\partial a} & = & -d_1(a)u_1(t,a) + D_2(a)u_2(t,a) - D_1(a)u_1(t,a) \\ \frac{\partial u_2(t,a)}{\partial t} + \frac{\partial u_2(t,a)}{\partial a} & = & -d_2(a)u_2(t,a) + D_1(a)u_1(t,a) - D_2(a)u_2(t,a) \end{cases} \tag{1.76}$$

where $u_i(t,a)$ is considered as the population density of the individuals at time t, age a and patch i.

Suppose one can simplify the continuous age-structured model into distinct age classes: mature and immature. Denote the maturation age by $r \geq 0$. Moreover, for $i = 1, 2$ assume that

$$d_i(a) = \begin{cases} d_{i,I}(a) & = & d_I(a) \text{ for } 0 \leq a \leq r, \\ d_{i,m}(a) & \equiv & \textit{constant} \text{ for } a > r, \end{cases} \tag{1.77}$$

and

$$D_i(a) = \begin{cases} D_{iI}(a) & = & D_I(a) \text{ for } 0 \leq a \leq r, \\ D_{im}(a) & \equiv & \textit{constant} \text{ for } a > r, \end{cases} \tag{1.78}$$

where I and m stand for infants (immature individuals) and adults (mature individuals).

The number of adults in patch i at time t is given by

$$w_i(t) = \int_r^\infty u_i(t,a)da \tag{1.79}$$

and since only adults can give birth

$$u_i(t,0) = b_i(w_i(t)), \tag{1.80}$$

where $b_i(w)$ is the birth rate of the species in the ith patch.

By integrating (1.76) with respect to a from r to ∞ we get

$$\frac{d}{dt}w_i(t) = u_i(t,r) - d_{i,m}w_i(t) + D_{j,m}w_2(t) - D_{i,m}w_1(t) \tag{1.81}$$

where it has been assumed $u_i(t,\infty) = 0$.

Furthermore, the method of integration along characteristics [61] can be used to obtain the formula for $u_i(t,r)$. The extension of this model to the general multi-patch case is given in [185]. Another extension is due to infinite discrete patches with discrete spatial diffusion and global interaction which gives us the following system of lattice delay differential equation

$$\frac{\partial}{\partial t}u_j(t,a) + \frac{\partial}{\partial a}u_j(t,a) = D(a)[u_{j+1}(t,a) + u_{j-1}(t,a) - 2u_j(t,a)] - d(a)u_j(t,a), \tag{1.82}$$

where $t > 0$, $j \in \mathbb{Z}$,$u_j(t,0) = b(w_j(t))$, $D(a)$ and $d(a)$ are respectively diffusion and death rates of the population at age a.

One can observe that the diffusion term in (1.82) is in discrete form, which means spatial diffusion occurs only at the nearest neighborhood and is proportional to the difference of the densities of the adjacent patches. Moreover, the patches are located at the integer nodes of a one-dimensional lattice.

Let diffusion and death rates be age independent (i.e. $D(a) = D_m$ and $d(a) = d_m$ for $a \in [r,\infty)$), then similar to the case above integrating from both sides of (1.82) and using (1.79) we obtain

$$\frac{dw_j(t)}{dt} = u_j(t,r) + D_m[w_{j+1}(t) + w_{j-1}(t) - 2w_j(t)] - d_m w_j(t) \text{ for } t > 0. \tag{1.83}$$

Then using discrete Fourier transformation and the method of integration along characteristics gives us the following formula for u_j

$$u_j(t,r) = \frac{\mu}{2\pi}\sum_{k=-\infty}^{\infty}\beta(j,k)b(w_k(t-r)), \tag{1.84}$$

where

$$\beta(j,k) = \int_{-\pi}^{\pi} \exp\left\{i[(j-k)w] - 4\alpha \sin^2(\frac{w}{2})\right\} dw. \tag{1.85}$$

Extension of the above process to continuous spatial domain was given by J. H. So et al [166]. The continuous model analogous to (1.82) is in the form of

$$\frac{\partial w}{\partial t} = D_m \frac{\partial^2 w}{\partial x^2} - d_m w + \frac{e^{\int_{-r}^{0} d_I(\theta)d\theta}}{\sqrt{4\pi\alpha}} \int_{-\infty}^{\infty} b(w(y,t-r))e^{\frac{-(x-y)^2}{4\alpha}} dy, \text{ for } t > r, \tag{1.86}$$

where $D(a) = D_m$ and $d(a) = d_m$ are respectively constant diffusion and death rates, d_I is the immature death rate, $r > 0$ is the maturation time and the term $\frac{1}{\sqrt{4\pi\alpha}} e^{\frac{-(x-y)^2}{4\alpha}}$ is the heat kernel.

Note that equation (1.86) is a nonlocal delayed RD equation. Therefore, both Britton's approach and the Smith-Thieme approach may give rise to the same class of nonlocal delay diffusive systems.

Our previous work [19] includes further details on modeling and traveling wave studies of delayed non-local RD Systems. The next section describes the objectives of the present work.

1.4 Statement of the main problem

In the present work we consider the nonlocal RD model proposed by So et al. [165]. Specifically, Smith-Thieme's approach was applied to a structured population model to obtain a functional differential equation for the matured population in a biological system with two age classes [161]. They derived the following RD equation with time delay and nonlocal effects

$$\frac{\partial w}{\partial t} = D_m \frac{\partial^2 w}{\partial x^2} - d_m w + \epsilon \int_{-\infty}^{\infty} b(w(y,t-\tau)) f_\alpha(x-y) dy, \tag{1.87}$$

where $x \in \mathbb{R}$, $0 < \epsilon \leq 1$. The term $w(x,t)$ represents the total mature population $u(x,a,t)$ at age a time t and position x that is given by

$$w(x,t) = \int_{\tau}^{\infty} u(x,a,t) da.$$

The kernel function is given by $f_\alpha(x) = \frac{1}{\sqrt{4\pi\alpha}} e^{-x^2/4\alpha}$ with $\alpha = \tau D_I > 0$, $\tau > 0$ is the maturation time, D_m and d_m are respectively the diffusion and death rate, D_I is the diffusion rate for the immature population and $b(u)$ is the nonlinear birth function. The total mature population at time t and location x is denoted by $w(t, x)$.

Here ϵ reflects the impact of the death rate for the immature population and corresponds to

$$\epsilon = \exp\left\{\int_{-\tau}^{0} d_I(\theta)d\theta\right\}. \tag{1.88}$$

As the immature population becomes immobile (i.e. when $\alpha \to 0$), equation (1.87) reduces to

$$\frac{\partial w}{\partial t} = D_m \frac{\partial^2 w}{\partial x^2} - d_m w + \epsilon b(w(x, t - \tau)). \tag{1.89}$$

Thus the nonlocal effect disappears as $\alpha \to 0$. Equation (1.89) has been widely studied for the case $\epsilon = 1$ and for different choices of $b(w)$ [119], [163], [165]. In equation (1.87) let $Y = y - x$ and $z = x + ct$. Define the linear transformation $T(t, x) := x + ct$. Let $w(x, t) = \phi(z)$ be the wave solution. Then substituting $\phi(z)$ into (1.87) using the transformation $T(t - \tau, y) = z - c\tau + Y$, replacing z with t and Y with y, the wave equation corresponding to (1.87) is given by

$$D_m\phi'' - c\phi' - d_m\phi + \epsilon \int_{-\infty}^{\infty} b(\phi(t - c\tau + y))f_\alpha(y)dy = 0. \tag{1.90}$$

The problem of existence of traveling wavefronts of (1.87) has been treated in several studies. Upper-lower solution method [75], [192], [110], [189], super-subsolution method [35], [36] and many other techniques have been employed to establish the existence and uniqueness. For instance, the following general form proposed by Ou and Wu covers a wide range of models including the model (1.87). The general delayed nonlocal RD system is presented by

$$\frac{\partial u(x,t)}{\partial t} = D\nabla^2 u(x,t) + F\left(u(x,t), \int_{-\tau}^{0}\int_{\Omega} d\mu_\tau(\theta, y)g(u(x + y, t + \theta))\right), \tag{1.91}$$

where $x \in \mathbb{R}^m$, $t \geq 0$, $u(x,t) \in \mathbb{R}^n$, $D = diag(d_1, \ldots, d_n)$ with positive constants d_i, $i = 1, \ldots, n$, $\tau > 0$, $\Omega \subset \mathbb{R}^m$, $\mu_\tau : [-\tau, 0] \times \Omega \to \mathbb{R}^{n\times n}$ is a normalized variation function (i.e. $\int_{-\tau}^{0}\int_{\Omega} d\mu_\tau(\theta, y) = 1$), $F : \mathbb{R}^n \times \mathbb{R}^n \to \mathbb{R}^n$ and $g : \mathbb{R}^n \to \mathbb{R}^n$ are C^2-smooth functions.

Ou and Wu established the existence of the traveling wavefronts of system (1.91) for the case that time lag τ is relatively small. In particular, let $\tau \to 0$; then system (1.91) is reduced to an RD system with no time delay. Suppose such a system admits traveling wavefronts, then it is very natural to ask if such wavefronts persist in the presence of time delay τ or they vanish as the system is perturbed by τ. Using a perturbation argument and the Fredholm alternative theory [139], the authors demonstrated that for $\tau > 0$ small, system (1.91) has a traveling wavefront as long as the reduced form of (1.91) with $\tau = 0$ has a wavefront. The biological implication of this result is that small time delays τ can be harmless in the sense that traveling wavefronts of the reduced form persist when time lag τ is incorporated in the form of system (1.91). Furthermore, the restriction on τ to be small enough for existence of traveling wavefronts can be removed for some special cases (e.g. [161]). This includes equation (1.87) under monostability and monotonicity conditions (i.e. the case that (1.90) has only two steady states $[\phi_1, \phi_2]$). There are also weaker conditions such as quasi-monotonicity or partially (exponentially) quasi-monotonicity applicable to the model (1.87) (see for example [75]). While existence and uniqueness results are great achievements in the study of traveling wave solutions, most works remain theoretical and do not discuss any practical method toward constructing the actual wave solution. Numerical solutions of the model and the corresponding wave equation can be very helpful in understanding the behavior of the wave solutions. Nevertheless, they are dependent on the set of the parameter values. Therefore, a numerical finding becomes more valuable when it is used to confirm a theoretical result rather than standing on its own.

The objectives of the present work are divided into three parts: local and global stability of steady states, stationary and traveling wave solutions and model development. It is known that the solutions of a differential equation are greatly influenced by the stability of steady states of that equation. The characteristic equations corresponding to equations (1.87) and (1.90) have infinitely many roots. Therefore, it becomes a nontrivial task to determine the stability of the steady states. We believe the stability analysis of (1.87) and (1.90) is the first step toward understanding the behavior of the wave solutions.

Regarding the wave solutions of (1.87), the main goal of the present work is to remain as practical as possible. We avoid non-constructive theoretical methods that lead only to existence and uniqueness of traveling wave solutions. There is no doubt that the problems connected to the real world demand further investigations on the local and global behavior of the wave solutions. Although finding the exact wave solution $\phi(t)$ of (1.87) is an extremely difficult task, at the very least we look for accurate approximations of the wave solutions that can be numerically verified. Moreover, the present work is not limited to the problem of traveling wavefronts; the stationary wave solutions of (1.87) are also investigated in detail. Model (1.87) is developed with respect to one-dimensional spatial domain $\mathbb{R}$. Then we are concerned with developing the model into a two-dimensional domain. Previous works on development of (1.87) include spatial domains of the form of rectangle and also strip. The present work develops the model (1.87) with respect to circular domain. The selections of spatial domain and also of boundary conditions are justified in the present work. Namely, circular domains have been frequently used in various laboratory experiments.

The contents of Chapters 2-5 are organized as follows. In Chapter 2 the stability analysis of model (1.87) and the wave equation (1.90) is provided for a general birth function $b(w)$. Also, considering a number of well-known birth functions, stability of steady states is determined. Using the method of Liapunov functions, it is shown that under some conditions the trivial solution is a global attractor of model (1.87).

In Chapter 3 periodic and nonperiodic stationary wave solutions of (1.90) are studied. With regard to specific birth functions, stationary wave pulses and stationary wavefronts are determined explicitly. In Chapter 4, traveling wave solutions of the model (1.87) are investigated in great detail; perturbation techniques, boundary layer methods, extended differential transform method and asymptotic expansion techniques are employed to obtain approximations of traveling wave solutions. Also, further steps are taken with respect to the monotone iterative method. Moreover, the creeping velocity of population expansion is briefly discussed. In Chapter 5, the model is developed with respect to a symmetrical spatial domain. Previous model developments are based on rectangular domains, whereas the present work considers a circular domain in which symmetry plays a role in derivation of the final model.

Chapter 2

Stability analysis

The main goal of the present chapter is to study the stability of steady states of the population model and the wave equation. This is of special interest since the study of traveling wave solutions requires primary knowledge about the stability of steady states. For instance, a traveling or stationary wavefront usually corresponds to a case that an unstable steady state is connected to a stable (or unstable) steady state through a solution of the wave equation. In the phase-plane of the wave equation this corresponds to a heteroclinic orbit connecting a saddle to a stable node (or to a saddle).

The contents of this chapter are organized as follows. Section 2.1 deals with basic definitions and preliminary matters. Section 2.2 is concerned with linearization and the characteristic equation. In Section 2.3 the specific birth functions are introduced and the positive steady states along with the related existence conditions are described. In Section 2.4 a local stability analysis of the model is provided. It is shown that under some conditions the stability of the steady states is independent of delay. In Section 2.5 it is demonstrated that under some conditions, the trivial solution is a global attractor of all positive solutions of the reduced model. In Section 2.6 local stability of steady states with respect to the wave equation is presented.

Essentially, a thorough treatment of the roots of the characteristic equation is given.

2.1 Preliminaries: stability of DDEs

The classical stability theory of Ordinary Differential Equations (ODEs) was generalized in the 1970s to investigate the stability of solutions of Retarded Functional Differential Equations (RFDEs) of the form

$$\dot{x}(t) = f(t, x_t), \tag{2.1}$$

where $x \in C([-\sigma - \tau, \sigma + A], \mathbb{R}^n)$ with $\sigma \in \mathbb{R}$ $\tau, A \geq 0$ and $t \in [\sigma, \sigma + A]$, $x_t \in C$ is defined as $x_t(\theta) = x(t + \theta)$ for $\theta \in [-\tau, 0]$, $f : \mathbb{R} \times C([-\tau, 0], \mathbb{R}^n) \to \mathbb{R}^n$.
Moreover, suppose that f is completely continuous (i.e. f takes closed bounded sets of $\mathbb{R} \times C([-\tau, 0], \mathbb{R}^n)$ into bounded sets of $\mathbb{R}^n$); then, as outlined in Chapter 5 pages 103-104 of [69], the stability of trivial solutions of (2.1) is defined as follows.

Definition 1. *Suppose $f(t, 0) = 0$ for all $t \in \mathbb{R}$. The solution $x = 0$ of equation (2.1) is said to be*

- *(i) stable if for any $\sigma \in \mathbb{R}, \epsilon > 0$, there is a $\delta = \delta(\epsilon, \sigma)$ such that $\phi \in \beta(0, \epsilon)$ implies $x_t(\sigma, \phi) \in \beta(0, \epsilon)$ for $t \geq \sigma$, where $\beta(0, \epsilon)$ is a ball of radius ϵ, centered at the origin.*

- *(ii) asymptotically stable if it is stable and there is a $b_0 = b_0(\sigma) > 0$ such that $\phi \in \beta(0, b_0)$ implies $x(\sigma, \phi)(t) \to 0$ as $t \to \infty$.*

- *(iii) uniformly stable if the number δ in the definition (i) is independent of σ.*

- *(iv) uniformly asymptotically stable if it is uniformly stable and there is a* $b_0 > 0$ *such that, for every* $\eta > 0$, *there is a* $t_0(\eta)$ *such that* $\phi \in \beta(0, b_0)$ *implies* $x_t(\sigma, \phi) \in \beta(0, \eta)$ *for* $t \geq \sigma + t_0(\eta)$ *for every* $\sigma \in \mathbb{R}$.

Stability of a general solution $y(t)$ of (2.1) is defined through the stability for the solution $z = 0$ of the equation

$$\dot{z}(t) = f(t, z_t + y_t) - f(t, y_t). \tag{2.2}$$

A usual approach in the study of Delay Differential Equations (DDEs) is to begin from local stability analysis of some special solutions (e.g. trivial or constant solutions). For this purpose, equations are linearized about the special solution. The stability of the special solutions (i.e. steady states) depends on the nature of the roots of the associated characteristic equation. For instance, the characteristic equation for the homogeneous linear delay differential equation

$$\dot{x}(t) = Ax(t) + Bx(t - \tau), \tag{2.3}$$

is given by

$$\lambda - A - Be^{-\lambda\tau} = 0, \tag{2.4}$$

where A and B are constants.

The following theorem gives an exponential bound on $x(t)$ in terms of $\max Re(\lambda)$ (i.e. maximum of the real part of solutions λ of (2.4)).

Theorem 1. If $\lambda_m = \max_\lambda Re(\lambda)$, then for any $\gamma > \lambda_m$, there is a constant $k = k(\gamma)$ such that solution $x(t)$ of (2.3) satisfies

$$|x(t)| \leq ke^{\gamma t}, t \geq 0$$

Proof.

The proof is given in Chapter 1, pages 20-21 of [69]. Basically, it uses the fundamental solution of (2.3) to derive the exponential bounds on $x(t)$. □

Hence, the trivial solution of (2.3) is asymptotically stable if $\lambda_m < 0$. This is the same as stability of ODEs. In fact a large class of DDEs can be linearized about their steady states and take the form of Equation (2.3). Then the local stability of steady states of DDEs can be determined from the roots of (2.4). From the following theorem we conclude that if there exists a root λ of (2.4) with $Re(\lambda) > 0$ then the corresponding steady state is unstable.

Theorem 2. Suppose λ is a root of (2.4) with multiplicity m. Then

$$x(t) = \sum_{k=0}^{m-1} a_k t^k e^{\lambda t}, \ a_k \in \mathbb{R},$$

is a solution of (2.3).

Proof.

It is only required to show that $t^k e^{\lambda t}$ is a solution of (2.3). Substituting $t^k e^{\lambda t}$ into (2.3), using the characteristic equation (2.4) and the binomial theorem, the result is obtained. The complete proof is given on page 18 of [69]. □

Despite the fact that RFDEs share many properties with ODEs (and also PDEs), we should emphasize that there are fundamental distinctions between the two theories. Namely, the linearized autonomous RFDEs define strongly continuous semi-groups on the phase space that are not analytic. In fact, the spectra of their generators consist of isolated eigenvalues with finite multiplicities. For instance, the linear delay differential equation

$$\dot{x}(t) = -\alpha x(t-\tau), \tag{2.5}$$

has the solution $x : t \to e^{\lambda t}$ if and only if λ is the root of the corresponding characteristic equation

$$\lambda + \alpha e^{-\lambda\tau} = 0. \tag{2.6}$$

Using Theorem 2, equation (2.5) has infinitely many solutions when $\tau > 0$; whereas the solution for the case $\tau = 0$ is only $x(t) = e^{-\alpha t}$. Moreover, only a finite number of eigenvalues may have a nonnegative real part. Therefore, the center and unstable manifolds of steady states are finite dimensional and the strongly continuous semi-group $\Gamma(t) = \exp(\alpha t)$ related to (2.5) is not analytic (See [183] for more details). Although in both DDEs and ODEs, the roots of the characteristic equations determine the local stability of the steady states corresponding to delay equations, it should be noted that the characteristic equations of DDES have infinitely many roots and it can be a highly nontrivial task to determine if all roots have negative real parts.

The next section will present the linearization process for the population model and its wave equation.

2.2 Linearization and the characteristic equations

In the previous chapter we introduced the following population model with its corresponding wave equation respectively,

$$\frac{\partial w}{\partial t} = D_m \frac{\partial^2 w}{\partial x^2} - d_m w + \epsilon \int_{-\infty}^{\infty} b(w(t-\tau, y)) f_\alpha(x-y) dy, \tag{2.7}$$

$$D_m \phi'' - c\phi' - d_m \phi + \epsilon \int_{-\infty}^{\infty} b(\phi(t - c\tau + y)) f_\alpha(y) dy = 0, \tag{2.8}$$

where $f_\alpha(y) = \frac{1}{\sqrt{4\pi\alpha}} e^{-y^2/4\alpha}$ is the one-dimensional heat kernel and $b(w)$ is a general birth function.

A basic method for studying the local stability of the steady states of a differential equation is linearization. In order to linearize equation (2.8) around the spatially constant steady state ϕ_j, let the solution ϕ in the neighborhood of ϕ_j be of the form of $\phi = \phi_j + \tilde{\phi}$. Then substituting this form into the equation (2.8), we get that,

$$D_m \tilde{\phi}'' - c\tilde{\phi}' - d_m(\tilde{\phi} + \phi_j) + \epsilon \int_{-\infty}^{\infty} b(\tilde{\phi}(t - c\tau + y) + \phi_j) f_\alpha(y) dy = 0. \tag{2.9}$$

Using Taylor expansion of b, dropping the nonlinear terms and considering that

$$\epsilon \int_{-\infty}^{\infty} b(\phi_j) f_\alpha(y) - d_m \phi_j = 0,$$

we have

$$D_m \tilde{\phi}'' - c\tilde{\phi}' - d_m \tilde{\phi} + \epsilon b'(\phi_j) \int_{-\infty}^{\infty} \tilde{\phi}(t - c\tau + y) f_\alpha(y) dy = 0. \tag{2.10}$$

In equation (2.10) let $\tilde{\phi}(t) = e^{\lambda t}$; then we get

$$D_m \lambda^2 - c\lambda - d_m + \epsilon b'(\phi_j) \int_{-\infty}^{\infty} e^{(-c\tau + y)\lambda} f_\alpha(y) dy = 0. \tag{2.11}$$

Noting that $\lambda y - \frac{1}{4\alpha} y^2 = -\frac{1}{4\alpha}(y - 2\alpha\lambda)^2 + \alpha\lambda^2$, the last integral is given by

$$I = \int_{-\infty}^{\infty} e^{(-c\tau + y)\lambda} f_\alpha(y) dy = e^{\alpha\lambda^2 - c\tau\lambda} \int_{-\infty}^{\infty} \frac{1}{\sqrt{4\pi\alpha}} \exp(\frac{-1}{4\alpha}(y - 2\alpha\lambda)^2) dy.$$

By letting $z = y - 2\alpha\lambda$, we have

$$I = e^{\alpha\lambda^2 - c\tau\lambda} \int_{-\infty}^{\infty} f_\alpha(z) dz = e^{\alpha\lambda^2 - c\tau\lambda}.$$

Hence, the characteristic equation corresponding to the wave equation (2.8) is given by

$$D_m \lambda^2 - c\lambda - d_m + \epsilon b'(\phi_j) e^{\alpha\lambda^2 - c\tau\lambda} = 0. \tag{2.12}$$

Following the same procedure for equation (2.7), we get the characteristic equation,

$$\lambda + d_m - \epsilon b'(\phi_j) e^{-\tau\lambda} = 0. \tag{2.13}$$

Note that, $\frac{\partial^2}{\partial x^2}(\phi_j + \tilde{\phi}) = 0$ and

$$\int_{-\infty}^{\infty} f_\alpha(x - y) dy = \int_{-\infty}^{\infty} f_\alpha(y - x) dy = 1.$$

In the next section we will obtain the specific steady states when certain birth functions are used in the model.

2.3 Specific birth functions and the steady states

As mentioned before, there are several birth functions $b(w)$ that can be considered in the population model (2.7). The stability of the steady states depends largely on the general birth function $b(w)$. Nevertheless, to compare the results with outcomes of the earlier studies we consider six different birth functions that have been widely used in several studies. These six birth functions represent large classes of density dependent reproduction dynamics of species. From an ecological point of view, the expected population a_{t+1} in generation $t+1$ is described as a function of population a_t in generation t. In the simplest approach, the population at each generation can be an increasing function of the population at the previous generation. The issue of unbounded population growth was first addressed by T. R. Malthus in 1798. Later in 1838, P. F. Verhulst [177], [178] attempted to resolve the issue by introducing a self-limiting mechanism that operates when a population becomes too large. Namely, Verhulst proposed the well-known logistic growth model. When the population becomes too large, the positive feedback effect of aggregation and cooperation can be dominated by a density-dependent stabilizing negative feedback effect due to intraspecific competition arising from excessive crowding and the ensuing shortage of resources. There are two main categories taking into account the concept of a self-limiting mechanism. The first one is the overcompensating density dependence in which the population is subject to decline after it reaches a maximum value. Alternately, a compensating density dependence results in monotonic increases in the population size until it reaches a steady state in a discrete sense.

In addition to the above-mentioned distinctions, the birth functions are classified as those with or without Allee effect [6], [7]. The main concept of the Allee effect is that a reduction in individual fitness at low population sizes leads to a reduction in per capita growth rate. Then mathematically, a birth function with Allee effect corresponds to a function with an inflection point. The birth functions considered in this study represent all of the above-mentioned ecological elements. These are specified as follows.

$$b_1(\phi) = p\phi e^{-a\phi^q},$$

$$b_2(\phi) = \frac{p\phi}{1 + a\phi^q},$$

$$b_3(\phi) = \begin{cases} p\phi(1 - \frac{\phi^q}{k_c^q}) & 0 \leq \phi \leq k_c \\ 0 & \phi > k_c, \end{cases}$$

$$b_4(\phi) = p\phi^2 e^{-a\phi},$$

$$b_5(\phi) = \frac{p\phi^2}{1 + a\phi},$$

$$b_6(\phi) = \frac{p\phi^2}{(1 + a\phi)^2}.$$

where p, q, a and k_c are all positive constants.

The plots of these birth functions are presented in Figure 2.1. The birth functions $b_1(\phi)$, $b_3(\phi)$, $b_4(\phi)$ exhibit overcompensating density dependence, while $b_5(\phi)$ and $b_6(\phi)$ respectively represent unbounded growth and compensating density dependence. Depending on the value of $q > 0$, $b_2(\phi)$ can exhibit either compensating or overcompensating density dependence. Regarding the Allee effect, only the birth functions $b_4(\phi)$ and $b_6(\phi)$ possess such quality. The above-mentioned factors can be seen in Figure 2.1. In the following, a short description of each birth function is provided.

The birth function $b_1(\phi)$ was initially proposed by Nicholson [132], [133] to describe the oscillatory fluctuations in population density of sheep blowfly *Lucilia cuprina.* The proposed model had a fairly good agreement with experimental data and therefore it was developed to capture additional elements of the population behavior over time. Namely, Gurney, Blythe and Nisbet [66] included a discrete

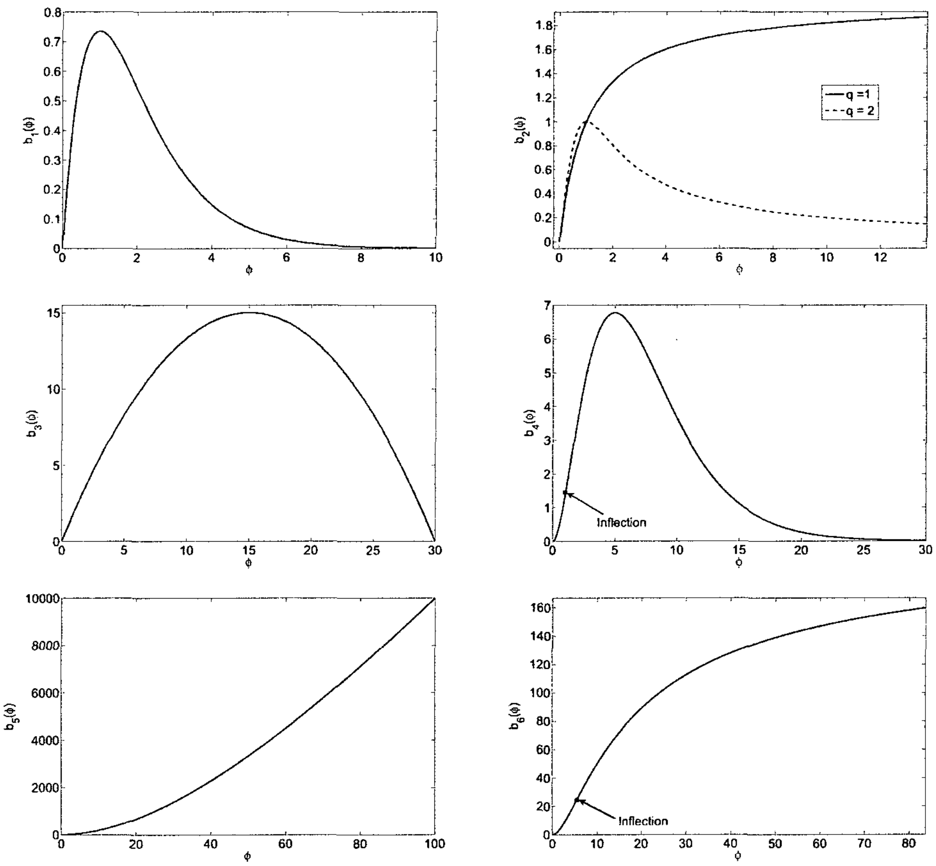


Figure 2.1: Plots of specific birth functions employed in the present study. Overcompensating and compensating density dependence, bounded and unbounded growth, presence and absence of Allee effect are all captured by these birth functions.

delay to a birth-death model and showed a "humped" relationship between future adult recruitment and current adult population of blowflies. In connection with spatial dispersion of blowflies, a diffusion term was added to the model and numerical Hopf bifurcation analysis [164], the Dirichlet problem [162] and the traveling wave solutions [102], [167] were studied in detail. Later the nonlocal effects were taken into account [165] and the model developed into equation (2.7). The birth function $b_2(\phi)$ with $q = 1$ was first proposed by Beverton & Holt [26] to study the dynamics of exploited fish populations. Similarly, the birth function $b_3(\phi)$ was introduced in management of fisheries and whaling. Namely, May [118] considered the first-order difference-delay equation,

$$N_t = (1-\mu)N_t + R(N_{t-T}), \tag{2.14}$$

with

$$R(N) = \frac{1}{2}(1-\mu)^T N(P + Q(1-(\frac{N}{k})^z)), \tag{2.15}$$

where N_t is the population of mature adult whales in year t, $(1-\mu)N_t$ is the surviving fraction and $R(N_{t-T})$ represents those newly recruited into adult population from birth T years ago (i.e. N_{t-T}).
Let $\mu = \frac{1}{2}(1-\mu)^T P$, then it can be shown that the discrete model (2.14) is changed to the continuous model

$$\frac{dN(t)}{dt} = -\mu N(t) + \mu N(t-\tau)(1 + r(1 - \frac{N(t-\tau)^z}{k^2})), \tag{2.16}$$

where $r = \frac{Q}{P}$.
Also, it can be shown that the last expression in (2.16) is equivalent to the birth function $b_3(\phi)$ when the problem is rescaled with

$$N = \frac{\phi}{1+r}, z = q \text{ and } k^q = \frac{rk_c^q}{(1+r)^{q+1}}.$$

The work of Liang and Wu [103] considers all three birth functions, $b_1(\phi)$, $b_2(\phi)$ and $b_3(\phi)$ and examines traveling waves and numerical approximations of the model

(2.7) with an extra advection term. Some other works develop the model with respect to two-dimensional spatial domains [186]. Existence of traveling waves is studied by taking into account the birth functions $b_1(\phi)$, $b_2(\phi)$ and $b_3(\phi)$.

The birth function $b_4(\phi)$ with $q = 1$ was first introduced by Asmussen [15]. Although with $q = 1$ the difference between $b_1(\phi)$ and $b_4(\phi)$ is only the square exponent in $b_4(\phi)$, choosing $b_1(\phi)$ or $b_4(\phi)$ in the model (2.7) makes huge differences from mathematical and ecological perspectives. Namely, the model (2.7) with $b_1(\phi)$ represents a monostable case (see Chapter 1) and includes only two steady states, while the model with $b_4(\phi)$ is categorized as a bistable case with three steady states which require a different approach for studying the corresponding traveling wave solutions. From an ecological perspective, the birth function $b_1(\phi)$ does not exhibit the Allee effect while $b_4(\phi)$ does. Later Aviles [16] used $b_4(\phi)$ to describe an ecological perspective on the evolution of sociality. The birth functions $b_5(\phi)$ and $b_6(\phi)$ are special cases of the population model derived by Eskola and Parvinen [41] by integrating a continuous time resource-consumer model. To include all possible cases of population activities, the birth function $b_5(\phi)$ is considered in this study which exhibits an unbounded population growth. The birth function $b_6(\phi)$ is based on overcompensating density dependence which presents Allee effect.

Note that steady states of (2.8) are the same as spatially homogeneous steady states of (2.7). Nevertheless, the stability changes from (2.7) to (2.8). The rest of this section is devoted to conditions for existence of non-negative steady states with respect to each birth function. Specifically, in order to be biologically meaningful, we restrict ourselves to nonnegative steady states. Noting that $\int_{-\infty}^{\infty} f_\alpha(x-y)dy = \int_{-\infty}^{\infty} f_\alpha(y)dy = 1$, a steady state of (2.8) (or (2.7)) is obtained by solving the equation $\epsilon b(\phi) = d_m \phi$ for $\phi \in \mathbb{R}$. With birth functions $b(\phi) = b_i(\phi)$, $i = 1, \ldots, 6$, one immediate steady state is the trivial solution $\phi_1 := 0$. When the birth functions b_4 or b_6 is considered we may have two positive steady states $0 < \phi_2 < \phi_3$. In all other

Table 2.1: A summary of positive steady states of (2.8) or (2.7)

birth function	condition for existence	positive steady state
b_1	$\epsilon p/d_m > 1$	$\phi_2 = (\frac{1}{a}\ln(\frac{\epsilon p}{d_m}))^{1/q}$
b_2	$\epsilon p/d_m > 1$	$\phi_2 = (\frac{\epsilon p - d_m}{a d_m})^{1/q}$
b_3	$\epsilon p/d_m > 1$	$\phi_2 = k_c(1 - \frac{d_m}{\epsilon p})^{1/q}$
b_4	$\epsilon p/d_m > ae$	$\phi_2, \phi_3 = -\frac{1}{a}W(-\frac{a d_m}{\epsilon p})$
b_5	$\epsilon p/d_m > a$	$\phi_2 = \frac{d_m}{\epsilon p - a d_m}$
b_6	$\epsilon p/d_m > 4a$	$\phi_2, \phi_3 = \frac{\epsilon p - 2a d_m \pm \sqrt{\epsilon p(\epsilon p - 4a d_m)}}{2a^2 d_m}$

cases, the equation (2.8) or (2.7) can admit only one positive steady state ϕ_2.

Table (2.1) represents the exact positive steady states ϕ_2 and ϕ_3 with their required conditions. The function W represented for b_4 is the Lambert W function which is defined as the inverse of the function $f(z) = ze^z$. Specifically, the equation

$$\epsilon p w e^{-aw} = d_m \tag{2.17}$$

is obtained by canceling w from both sides of $\epsilon b_4(w) = d_m w$. Then letting $z = -aw$ and solving (2.17) for z will give rise to positive steady states of (2.7) (or equivalently (2.8)). Note that in our case, W has two separate values. This is due to the fact that $W(x)$ is multiple valued for any $x \in (-e^{-1}, 0)$. When $\frac{\epsilon p}{d_m} = ae$, The two steady states merge together.

To explain this from a different perspective, define the function $g : \mathbb{R} \to \mathbb{R}$ as follows.

$$g(w) := \epsilon p w e^{-aw}. \tag{2.18}$$

Taking the derivative of g with respect to w we have,

$$g'(w) = \epsilon p e^{-aw}(1 - aw). \tag{2.19}$$

Hence, $w = \frac{1}{a}$ is a local maximum and $g_{max} = \frac{\epsilon p}{ae}$ is the maximum value. We conclude that equation (2.17) has two solutions when $\frac{\epsilon p}{ae} > d_m$. A schematic representation of equation (2.17) and the corresponding Lambert W function with possible solutions is given in Figure 2.2. Note that the intersection of the line with the curve represents a solution.

Remark 1. For the cases $i = 1, 2, 3$ the positive steady state approaches the zero steady state as $\frac{\epsilon p}{d_m} \to 1$. Similarly, for $i = 4$ (and $i = 6$), the two positive steady states merge when $\frac{\epsilon p}{d_m} \to ae$ ($\frac{\epsilon p}{d_m} \to 4a$).

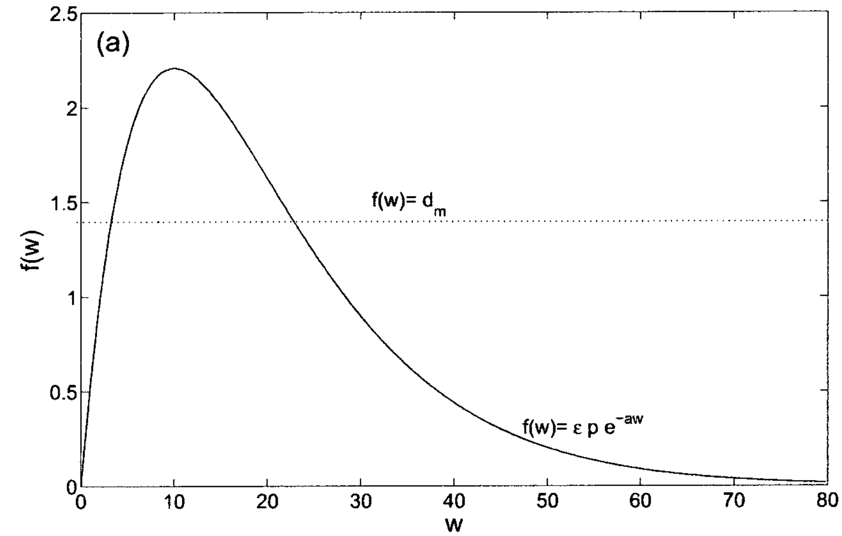
Remark 2. For the case $i = 5$, the positive steady state vanishes when $\frac{\epsilon p}{d_m} \to a$.

For the cases $i = 1, 2, 3$ when $\frac{\epsilon p}{d_m} < 1$, we may think of negative steady states when $q^{-1} = 2k + 1$, $k \in \mathbb{Z}$. Moreover, when equation (2.17) is solved in $\mathbb{C}$ (complex numbers), condition $q^{-1} = 2k$, $k \in \mathbb{Z} \setminus \{0\}$ gives rise to positive steady states. This is due to the fact that the equation (2.17) is reduced to $\sqrt[2k]{w} = N$, where N is a negative number. Nonetheless in this chapter, we are only concerned with nonnegative steady states obtained by considering the real domain. We have the following lemma.

Lemma 1. Let $\frac{\epsilon p}{d_m} > \max\{1, 4a\}$. Then equation (2.7) with the birth function $b_i(\phi)$ for $i = 1, \ldots, 6$ and therefore equation (2.8) has at least one positive steady state.

Proof.

As outlined in Table 2.1, the positive steady states ϕ_j are calculated directly from $\epsilon b_i(\phi) = d_m\phi$. $\square$



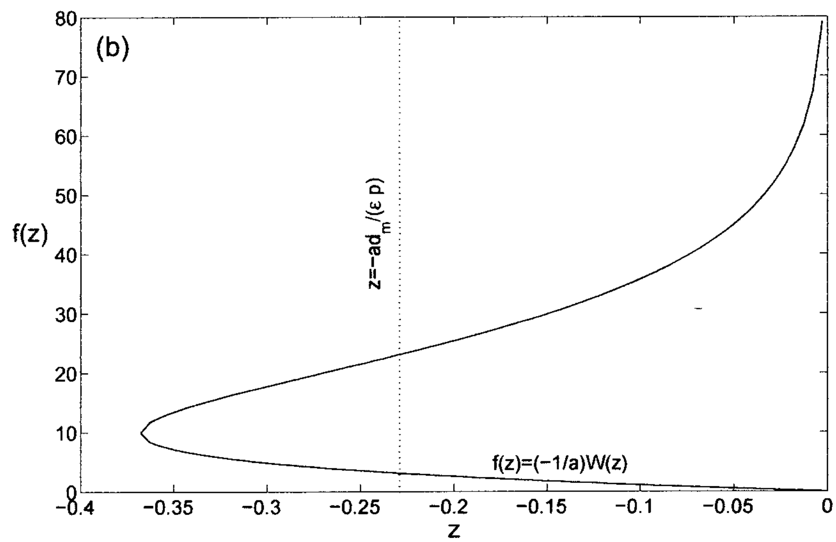


Figure 2.2: a) graph of $f(w) = \epsilon p w e^{-aw}$ and $f(w) = d_m$. b)using Lambert W function, the possible solutions of $\epsilon p w e^{-aw} = d_m$ are the intersections of the line $z = \frac{-ad_m}{\epsilon p}$ and the curve $f(z)$.

The next section is concerned with local stability of steady states arising from model (2.7).

2.4 Local stability analysis of the model

In this section we study the local stability and the effect of delay on the stability of the homogeneous (i.e. $D_m = 0$) steady state ϕ_j (2.7). The main question is whether there will be any stability switches when delay is introduced to the system. The following theorem shows that under some conditions the stability of ϕ_j is independent of delay $\tau \geq 0$

Theorem 3. If $\epsilon|b^{'}(\phi_j)| < d_m$, then for all $\tau \geq 0$ the homogeneous steady state ϕ_j of (2.7) is asymptotically stable.

Proof.

When $\tau = 0$ the characteristic equation (2.13) is reduced to $\lambda = \epsilon b^{'}(\phi_j) - d_m$. Hence ϕ_j is asymptotically stable. Let $\tau > 0$. Assume that the characteristic equation (2.13) has a root $\lambda = u + iv$ where $u \geq 0$ for some $\tau > 0$. Substituting $\lambda = u + iv$ into (2.13) and equating the real part and the imaginary part to zero we get that

$$u + d_m - \epsilon b^{'}(\phi_j)e^{-u\tau}\cos(\tau v) = 0, \tag{2.20}$$

$$v + \epsilon b^{'}(\phi_j)e^{-u\tau}\sin(\tau v) = 0. \tag{2.21}$$

Moving the terms with sine and cosine to the righthand side, squaring them and adding them together, we obtain

$$(u + d_m)^2 + v^2 = \epsilon^2 b'^2(\phi_j)e^{-2u\tau}. \tag{2.22}$$

Since $\tau, u \geq 0$ we get that

$$(u + d_m)^2 + v^2 \leq \epsilon^2 b'^2(\phi_j). \tag{2.23}$$

Expanding the first term in (2.23) we have

$$u^2 + 2ud_m + v^2 \leq \epsilon^2 b'^2(\phi_j) - d_m^2. \tag{2.24}$$

Since $u \geq 0$, the lefthand side of (2.24) is positive whereas the righthand side of (2.24) is negative due to $\epsilon|b'(\phi_j)| < d_m$. This is a contradiction.□

In the following, we will take an alternative approach to prove a result stronger than Theorem 3. First we state a theorem due to Hayes [72]; that is given in the book by Hale [69].

Theorem 4 (Hayes). All roots of the equation

$$(z + A)e^z + B = 0, \tag{2.25}$$

where $A, B \in \mathbb{R}$, have negative real parts if and only if,

H1) $A > -1$,

H2) $A + B > 0$,

H3) $B < \eta \sin(\eta) - A\cos(\eta)$, where η is the root of $\eta = -A\tan(\eta)$, $0 < \eta < \pi$ when $A \neq 0$ and $\eta = \frac{\pi}{2}$ if $A = 0$.

Proof.

The proof is based on the work by Bellman and Cooke [24] and it is found on Page 339-340 of [69]. □

Using Hayes theorem the necessary and sufficient condition for asymptotic stability of ϕ_j is given below.

Theorem 5. The homogeneous steady state ϕ_j of (2.7) is asymptotically stable if and only if

$$\epsilon|b'(\phi_j)| < d_m.$$

Proof.

The characteristic equation is given by,

$$\lambda + d_m - \epsilon b^{'}(\phi_j)e^{-\tau\lambda} = 0. \tag{2.26}$$

When $\tau = 0$, the asymptotic stability of ϕ_j is directly obtained from the fact that $\lambda = \epsilon b^{'}(\phi_j) - d_m < 0$. When $\tau > 0$, equation (2.26) is multiplied by $\tau e^{\tau\lambda}$ and we get that

$$(\tau\lambda + \tau d_m)e^{\tau\lambda} - \tau\epsilon b_i^{'}(\phi_j) = 0. \tag{2.27}$$

Define $z := \tau\lambda$, $A := \tau d_m$ and $B := -\tau\epsilon b^{'}(\phi_j)$. Then equation (2.27) is transformed to equation (2.25). Obviously the conditions **H1** and **H2** are satisfied when $\epsilon b^{'}(\phi_j) - d_m < 0$. Since $\eta \in (0, \pi)$ is the root of $\tan\eta = -\frac{\eta}{A}$ it can be easily shown that η must be in the interval $\left(\frac{\pi}{2}, \pi\right)$. Noting that $\eta = -A\tan(\eta)$, condition **H3** is equivalent to $B < \frac{-A}{\cos(\eta)}$. But this is obvious since $\epsilon|b^{'}(\phi_j)| < d_m$ and $\frac{-1}{\cos(\eta)} \in (1, \infty)$ for $\eta \in \left(\frac{\pi}{2}, \pi\right)$. All conditions of Theorem 4 are satisfied and the proof is complete. □

A major result of the Theorem 5 is that asymptotic stability of ϕ_j is independent of changes in delay if and only if $\epsilon|b^{'}(\phi_j)| < d_m$. But what happens when $\epsilon|b^{'}(\phi_j)| > d_m$? This is considered in two different cases.

Case 1: $\epsilon b^{'}(\phi_j) - d_m > 0$

When $\tau = 0$, ϕ_j is unstable and we show that it remains unstable for $\tau > 0$. In fact, the characteristic equation (2.13) admits a real positive root for $\tau > 0$. Define

$$h_j(\lambda) := \lambda + d_m - \epsilon b'(\phi_j)e^{-\tau\lambda} = 0. \tag{2.28}$$

Obviously $h_j(\lambda) = 0$ represents the characteristic equation (2.13) corresponding to the steady state ϕ_j. Since $\epsilon b_i'(\phi_j) - d_m > 0$, we have $h_j(0) < 0$. Moreover, the magnitude of the exponential term in (2.28) is a decreasing function of $\lambda \geq 0$. Then by the continuity of $h_j(\lambda)$ with respect to λ, we get that h_j has a real positive root.

Case 2: $\epsilon b'(\phi_j) + d_m < 0$

In this case, the stability of ϕ_j is delay-dependent. Here, we take advantage of some previous works. The birth function $b_1(u) = pue^{-a^{u^q}}$ with $q = 1$, proposed by Nicholson [132], [133] has received a lot of attention since the time it was used in a delay model of laboratory insect population derived by Gurney et al. [66]. In particular the model is given by

$$\frac{du(t)}{dt} = -d_m u(t) + \epsilon p u(t-\tau) e^{-au(t-\tau)}. \tag{2.29}$$

Observe that this is a reduced form of the population model (2.7). Namely, by letting $\alpha = 0$, $D_m = 0$, $w(t, \cdot) = u(t)$ and $b(u) = b_1(u)$ for $q = 1$, equation (2.7) is reduced to equation (2.29). Local and global stability of (2.29) has been discussed in various studies [45], [106], [105], [44]. It can be easily verified that the steady states of (2.29) are $E_1 = 0$ and $E_2 = \frac{1}{a} \ln \frac{\epsilon p}{d_m}$. Here the condition $\epsilon b'(\phi_j) + d_m < 0$ is equivalent to $\frac{\epsilon p}{d_m} > e^2$. The work by Faria et al. ([44], page35) states that if $\frac{\epsilon p}{d_m} > e^2$ then "the asymptotic stability of E_2 holds only when delay τ is sufficiently small". Note that the characteristic equation corresponding to equation (2.29) is the same as equation (2.13) with birth the function b_1 and $\alpha \geq 0$. To be more precise we bring the argument presented in [44].

The authors let $\lambda = i\omega$, $\omega \in \mathbb{R}$ and from (2.13) they obtain

$$i\omega = -d_m + \epsilon b_1'(E_2)(\cos(\omega\tau) - i\sin(\omega\tau)), \tag{2.30}$$

where $\epsilon b_1'(E_2) = d_m(1 - \ln \frac{\epsilon p}{d_m})$.

Separating (2.30) into imaginary and real parts we have

$$\left\{ \begin{array}{rcl} d_m & = & \epsilon b_1'(E_2)\cos(\omega\tau), \\ \omega & = & \epsilon b_1'(E_2)\sin(\omega\tau). \end{array} \right. \tag{2.31}$$

Squaring these two equations and adding them together we have,

$$\omega^2 = \epsilon b_1'^2(E_2) - d_m^2. \tag{2.32}$$

By choosing $\omega > 0$ we get that

$$\begin{aligned} \omega &= \sqrt{\epsilon b_1'^2(E_2) - d_m^2}, \\ &= d_m\sqrt{\left(\ln\frac{\epsilon p}{d_m} - 1\right)^2 - 1}. \end{aligned} \tag{2.33}$$

Substituting (2.33) into the first equation of (2.31) and solving for τ we get the following solutions.

$$\hat{\tau} = \frac{\pi - \arccos\frac{-d_m}{\epsilon b'(E_2)}}{\sqrt{\epsilon b'^2(E_2) - d_m^2}}, \tag{2.34}$$

Considering the specific form of the birth function $b(u) = b_1(u)$, $\hat{\tau}$ is given by

$$\hat{\tau} = \frac{\pi - \arccos\left(\left(\ln\frac{\epsilon p}{d_m} - 1\right)^{-1}\right)}{d_m\sqrt{\left(\ln\frac{\epsilon p}{d_m} - 1\right)^2 - 1}}. \tag{2.35}$$

Then the authors of [44] conclude that if $\frac{\epsilon p}{d_m} > e^2$ then for $\tau = \hat{\tau}$, the characteristic equation (2.13) has a pure imaginary root $\lambda = i\omega$ and therefore E_2 cannot be asymptotically stable.

In fact, the same argument can be used for a general birth function $b(\phi)$. This is summarized as follows. Let $\epsilon b'(\phi_j) + d_m < 0$ then ϕ_j is asymptotically stable only if $\tau < \hat{\tau}$, where $\hat{\tau}$ is defined in (2.34). This makes sense when Hayes Theorem 4 is considered. In particular, conditions **H1** and **H2** are directly satisfied. Since $\tan\eta = -\frac{\eta}{\tau d_m}$, we have $\eta \to \frac{\pi}{2}$ as $\tau \to 0$. Hence, condition **H3** is guaranteed as τ approaches to zero.

Consider equation (2.7) with specific birth functions $b_i(\phi)$ for $i = 1, \ldots, 6$. Let $\phi_1 = 0$ and $\phi_3 > \phi_2 > 0$ be the steady states of (2.7). Then we have the following lemma.

Lemma 2. In equation (2.7) let $\tau = 0$, if $\frac{\epsilon p}{d_m} > \max\{1, 4a\}$ for $j = 2, 3$ then the spatially homogeneous steady states ϕ_1 for $i = 1, 2, 3$ and ϕ_2 for $i = 4, 5, 6$ are unstable, while ϕ_1 for $i = 4, 5, 6$, ϕ_2 for $i = 1, 2, 3$ and ϕ_3 for $i = 4, 6$ are asymptotically stable.

Proof.

Using (2.13), when $\tau = 0$, the only eigenvalue corresponding to equation (2.7) is given by $\lambda_j = \epsilon b_i'(\phi_j) - d_m$ for $i = 1, \ldots, 6$, $j = 1, 2, 3$.

Hence $\lambda_j > 0$ implies that ϕ_j is unstable while $\lambda_j < 0$ means that ϕ_j is asymptotically stable.

Case $i = 1$

$$b_1'(\phi_1) = p, b_1'(\phi_2) = \frac{d_m}{\epsilon}(1 - q \ln \frac{\epsilon p}{d_m})$$
$$\lambda_1 = \epsilon p - d_m, \lambda_2 = -d_m q \ln \frac{\epsilon p}{d_m}$$

Case $i = 2$

$$b_2'(\phi_1) = p, b_2'(\phi_2) = \frac{1}{p}(\frac{d_m}{\epsilon})^2(\frac{\epsilon p}{d_m}(1 - q) + q)$$
$$\lambda_1 = \epsilon p - d_m, \lambda_2 = d_m q(-1 + \frac{d_m}{\epsilon p})$$

Case $i = 3$

$$b_3'(\phi_1) = p, b_3'(\phi_2) = -pq + \frac{d_m}{\epsilon} + q\frac{d_m}{\epsilon}$$
$$\lambda_1 = \epsilon p - d_m, \lambda_2 = \epsilon pq(-1 + \frac{d_m}{\epsilon p})$$

Hence in all cases 1,2 and 3, $\frac{\epsilon p}{d_m} > 1$ implies that $\lambda_1 > 0$ and $\lambda_2 < 0$.

Case $i = 4$

The derivative is given by $b_4'(\phi) = pe^{-a\phi}\phi(2 - a\phi)$, then $\lambda_1 = -d_m < 0$. From (2.18) and (2.19) we conclude that $0 < \phi_2 < \frac{1}{a} < \phi_3$. Also, from (2.17) we have $\epsilon b_4'(\phi_j) - d_m = d_m(1 - a\phi_j)$ for $j = 2, 3$. Then $\lambda_2 > 0$ while $\lambda_3 < 0$.

Case $i = 5$

The derivative is given by $b_5'(\phi) = \frac{p\phi(2+a\phi)}{(1+a\phi)^2}$, then $\lambda_1 = -d_m < 0$.

Noting that $\frac{\epsilon p \phi_2}{1+a\phi_2} = d_m$ we have $\lambda_2 = \epsilon b_5'(\phi_2) - d_m(\frac{1}{1+a\phi_2}) > 0$. Hence, ϕ_2 is unstable.

Case $i = 6$

The derivative is given by $b_6'(\phi) = \frac{2p\phi}{(1+a\phi)^3}$, then $\lambda_1 = -d_m < 0$. Noting that $\frac{\epsilon p\phi_j}{(1+a\phi_j)^2} = d_m$ for $j = 2, 3$ we have $\lambda_j = \epsilon b_6'(\phi_j) - d_m = \frac{d_m(1-a\phi_j)}{1+a\phi_j}$, $j = 2, 3$. But we have $\phi_3 > \frac{\epsilon p}{2a^2 d_m} - \frac{1}{a} > \phi_2$ and $\frac{\epsilon p}{d_m} > 4a$. Hence $\phi_3 > \frac{1}{a}$ and since $\inf_{\epsilon p/d_m}\{\frac{\epsilon p}{2a^2 d_m} - \frac{1}{a}\} \geq \phi_2$ we get that $\frac{1}{a} > \phi_2$. we conclude that $\lambda_2 > 0$ while $\lambda_3 < 0$.

This completes the proof. □

Remark 3. In Lemma 2, the condition $\frac{\epsilon p}{d_m} > \max\{1, 4a\}$ guarantees the existence of the steady states ϕ_2 and ϕ_3. The steady state ϕ_1 exists in any cases and it is independent of this condition.

Table (2.2) represents a summary of stability or instability of steady states ϕ_1, ϕ_2 and ϕ_3 of (2.7).

Table 2.2: Stability of homogeneous steady states ϕ_j of (2.7) for $\alpha \geq 0, \tau = 0$

Birth function	condition for existence	ϕ_1	ϕ_2	ϕ_3
b_1	$\epsilon p/d_m > 1$	U	AS	–
b_2	$\epsilon p/d_m > 1$	U	AS	–
b_3	$\epsilon p/d_m > 1$	U	AS	–
b_4	$\epsilon p/d_m > ae$	AS	U	AS
b_5	$\epsilon p/d_m > a$	AS	U	–
b_6	$\epsilon p/d_m > 4a$	AS	U	AS

Note: AS = asymptotically stable, U = unstable

Corollary 1. Let $\min\{e^{\frac{2}{q}}, \frac{q+2}{q}, \frac{q}{q-2}\} > \frac{\epsilon p}{d_m} > \max\{1, 4a\}$. For i=4, let $W(\frac{-ad_m}{\epsilon p}) > -3$. then for any $\tau \geq 0$ and $\alpha \geq 0$, ϕ_1 for $i = 1, 2, 3$ and ϕ_2 for $i = 4, 5, 6$ are unstable, while ϕ_1 for $i = 4, 5, 6$, ϕ_2 for $i = 1, 2, 3$ and ϕ_3 for $i = 4, 6$ are asymptotically stable.

Proof.

For ϕ_1, using Lemma 2, case 1 for $\epsilon b'(\phi_j) - d_m > 0$ and Theorem 3, the result is directly obtained. For ϕ_2 the upper bound for $\frac{\epsilon p}{d_m}$, case 1 and Theorem 3 give rise to the results. For ϕ_3, when b_4 is considered, $W(\frac{-ad_m}{\epsilon p}) > -3$ is used to complete the proof. $\square$

Remark 4. In Lemma 2 and Corollary 1, the condition $\frac{\epsilon p}{d_m} > \max\{1, 4a\}$ can be relaxed with $\frac{\epsilon p}{d_m} > 1$ for $i = 1, 2, 3$; $\frac{\epsilon p}{d_m} > ae$ for $i = 4$; $\frac{\epsilon p}{d_m} > a$ for $i = 5$ and $\frac{\epsilon p}{d_m} > 4a$ for $i = 6$.In Corollary 1, the upper bound for $\frac{\epsilon p}{d_m}$ can be replaced with $e^{\frac{2}{q}} > \frac{\epsilon p}{d_m}$ for $i = 1$, $\frac{q}{q-2} > \frac{\epsilon p}{d_m}$ for $i = 2$ and $\frac{q+2}{q} > \frac{\epsilon p}{d_m}$ for $i = 3$. These bounds violate the monotonicity condition (i.e. the ϕ_2 is greater and the local maximum of the corresponding birth function). For the monotonicity , it is required to replace the value 2 with 1 in each of these upper bounds.

Remark 5. According to Theorem 3, for a general birth function b, the general stability (instability) condition for ϕ_j in Lemma 2 and Corollary 1 is given by $\epsilon b'(\phi_j) - d_m < (>)0$.

So far we have ignored the effects of spatial variations. In the following we investigate the effects of diffusion on stability of steady states. Does diffusion have destabilizing effects on stability or does it stabilize the unstable steady states? The former case is known as Turing instability or diffusion driven stability where spatial patterns arise from a steady state of an RD system that is stable in absence of diffusion but becomes unstable when diffusion is introduced. In our previous studies [17], [20], [18], [21] we demonstrated the relevance of neurite spontaneous symmetry breaking with Turing instabilities in a proposed RD model of interacting signaling pathways. In what follows we will show that in the population model (2.7), diffusion has stabilizing effects and the model (2.7) does not exhibit any Turing instability. A solution of (2.7) in a neighborhood of the steady state ϕ_j has the form

$$W(t,x) \propto \exp(\lambda t + ik), \tag{2.36}$$

where λ is a root of the characteristic equation

$$\lambda + d_m + D_m k^2 - \epsilon b^{'}(\phi_j)e^{-\tau\lambda} = 0, \tag{2.37}$$

and $k \in \mathbb{R}$ is the wave number.

In fact expression (2.36) is obtained by solving equation (2.7) linearized about the steady state ϕ_j. It should be noted that the wave number k is not restricted to discrete numbers. Since the spatial domain is unbounded the wave number k corresponds to the eigenvalue problem

$$D_m \frac{\partial^2 w}{\partial x^2} + k^2 w = 0, \tag{2.38}$$

without any boundary conditions. Hence, k can be any real number.

We have the following theorem.

Theorem 6. Let $D_m > 0$, then the steady state of ϕ_j of (2.7) is asymptotically stable if and only if

$$\epsilon|b^{'}(\phi_j)| < d_m.$$

Proof.

Let $\tau = 0$. Considering the characteristic equation (2.37), for all $k \in \mathbb{R}$, ϕ_j is stable when $\epsilon b^{'}(\phi_j) - d_m < 0$. For the case $\tau > 0$, the proof is similar to that of Theorem 5. $\square$

Hence neither delay nor diffusion play any role in asymptotic stability of ϕ_j.

When $\epsilon b^{'}(\phi_j) - d_m > 0$, the steady state ϕ_j is unstable, but there exists $k_0 \in \mathbb{R}$

such that for all $k^2 > k_0^2$ the modes are stable. In other words ϕ_j becomes stable when the magnitude $|k|$ is sufficiently large. In a bounded spatial domain, the size of the domain plays a major role in having any spatial inhomogeneity (see [126] for more details). Note that a solution of the form (2.36) is local and it is only valid in a neighborhood of ϕ_j. When quation (2.7) evolves from ϕ_j, the nonlinear and nonlocal terms may mitigate the exponential growth of (2.36). If a global solution of (2.7) is bounded and non-oscillatory for all $t > 0$, then it is expected that the solution is attracted by an attractor as times increases. The other case is existence of a wavefront or wave pulse that can travel in the spatial domain or it can be stationary. In the next section existence of a global attractor of the model is discussed. Also we will investigate stationary wave solutions in the upcoming chapter.

2.5 A global attractor of the model

As mentioned before, the general form of the population model is given by

$$\frac{\partial w}{\partial t}(t,x) = D_m \frac{\partial^2 w}{\partial x}(t,x) - d_m w(t,x) + \epsilon \int_{-\infty}^{\infty} b(w(t-\tau,y)) f_\alpha(x-y)dy, \quad (2.39)$$

with initial history function

$$w(s,x) = g(s,x), x \in \mathbb{R}, s \in [-\tau, 0].$$

The main purpose of this section is to study the global stability of the trivial solution of (2.39). As shown in Lemma 2 and Theorem 3, the homogeneous (i.e. $D = 0$) steady state ϕ_j of (2.39) is locally asymptotically stable when

H1. $\epsilon \left|b'(0)\right| < d_m$,

Consider the following two conditions:

H2. $0 < b(w(t)) \leq b'(0)w(t)$, for all $t > -\tau$,

H3. $\epsilon b'(0)\tau < 1$. We will employ the method of Liapunov functional to establish global stability of $\phi_1 = 0$. We also use the next lemma that is due to Barbalat [22].

Lemma 3. Let f be nonnegative function defined on $[0, \infty)$ such that f is integrable on $[0, \infty)$ and uniformly continuous on $[0, \infty)$. Then $\lim_{t \to \infty} f(t) = 0$.

Proof.

The proof is given in Chapter 1, page 5 of [57]. $\square$

Concerning the global stability of the trivial solution, we have the following Theorem.

Theorem 7. Let $D_m = 0$, $\alpha = 0$, if **H1**, **H2** and **H3** are satisfied then all positive solutions of (2.39) have the asymptotic behavior

$$\lim_{t \to \infty} w(t) = 0$$

Proof.

When $D_m = 0$ and $\alpha = 0$ equation (2.39) is reduced to

$$\frac{dw(t)}{dt} = -d_m w(t) + \epsilon b(w(t - \tau)). \tag{2.40}$$

Using the fundamental theorem of calculus, the equation (2.40) can be written as

$$\frac{d}{dt}[w(t) + \epsilon \int_{t-\tau}^{t} b(w(s))ds] = -d_m w(t) + \epsilon b(w(t)). \tag{2.41}$$

Define the functional $V = V(w)(t)$ by

$$V(w)(t) = (w(t) + \epsilon \int_{t-\tau}^{t} b(w(s))ds)^2. \tag{2.42}$$

Taking the derivative of V with respect to t and using (2.41) we see that

$$\begin{aligned} \frac{dV}{dt} &= 2(-d_m w(t) + \epsilon b(w(t)))(w(t) + \epsilon \int_{t-\tau}^{t} b(w(s))ds) \\ &= 2(\epsilon b(w(t))w(t) - d_m w^2(t)) + 2\epsilon \int_{t-\tau}^{t} (\epsilon b(w(t)) - d_m w(t))b(w(s))ds \end{aligned} \tag{2.43}$$

From **H1** and **H2** we get that

$$\frac{dV}{dt} \leq 2(\epsilon b'(0) - d_m)w(t)^2 + 2\epsilon(\epsilon b'(0) - d_m) \int_{t-\tau}^{t} w(t)b(w(s))ds \leq 0 \tag{2.44}$$

Since $\frac{dV}{dt} \leq 0$, we get that V is a nonincreasing function with respect to t. Hence,

$$0 \leq V(w)(t) \leq V(w)(0) \tag{2.45}$$

From the equation (2.42) and inequality (2.45) we have

$$|w(t)| - \left| \epsilon \int_{t-\tau}^{t} b(w(s))ds \right| \leq (V(w)(t))^{\frac{1}{2}} \leq (V(w)(0))^{\frac{1}{2}}. \tag{2.46}$$

Hence

$$|w(t)| \leq (V(w)(0))^{\frac{1}{2}} + \epsilon \int_{t-\tau}^{t} |b(w(s))| \, ds. \tag{2.47}$$

For all solutions $w(s) > 0$ define

$$m(t) := \sup_{[t-\tau,t]} w(s)$$

Then using **H2**, **H3** and $w(s) \leq m(t)$, for all positive solutions w we have

$$0 \; < \; (1 - \epsilon b'(0)\tau)m(\tau) \; \leq \; (V(w)(0))^{\frac{1}{2}} \tag{2.48}$$

Hence, any solution $w(t) > 0$ is bounded on $[0, \infty)$. Using (2.40) it follows that $\frac{dw}{dt}$ is also bounded on $[0, \infty)$. Therefore, $w(t) > 0$ is uniformly continuous. Moreover, integrating (2.44) we have

$$\begin{aligned} V(w)(t) + 2(d_m - \epsilon b'(0)) \textstyle\int_0^t w^2(z)dz + \; 2(d_m - \epsilon b'(0)) \int_0^t \int_{t-\tau}^t w(z)b(w(s))dsdz \\ \leq V(w)(0) + k, \end{aligned} \tag{2.49}$$

where $k > 0$ is a constant. Hence w^2 is integrable. Using the the previous lemma we get that $w^2(t)$ (and therefore $w(t)$) tends to zero as $t \to \infty$. This completes the proof. □

Remark 6. In Theorem 7 the conditions **H2** and **H3** are equivalent to $\epsilon p/d_m < 1$ and $\epsilon p\tau < 1$ respectively when the birth function b_1, b_2 or b_3 is considered.

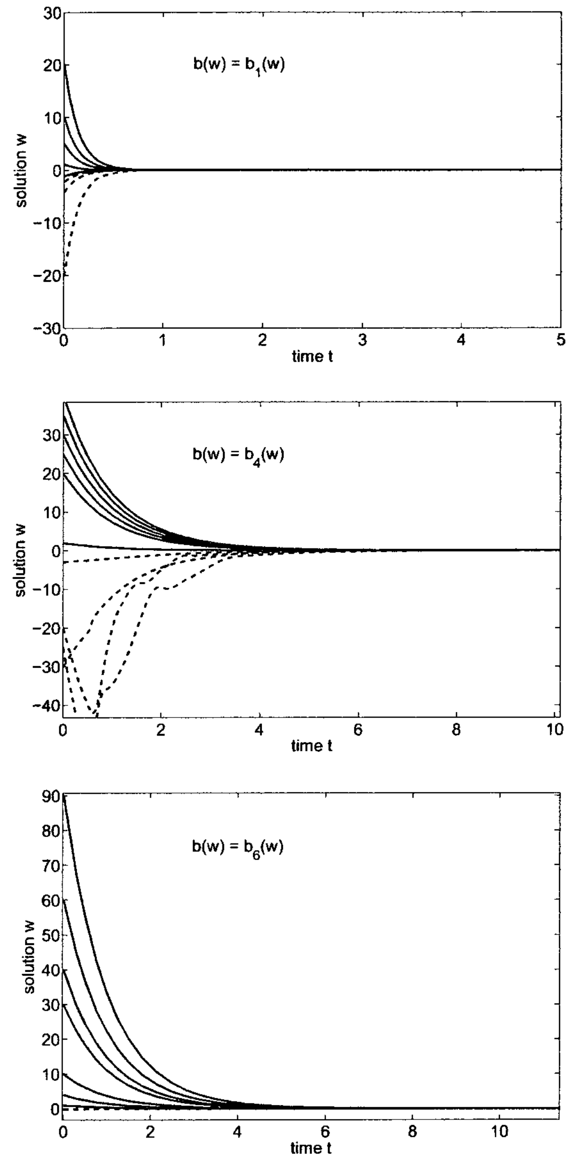


Figure 2.3: A representation of global attractivity of the trivial solution with different birth functions. From top to bottom the birth functions $b_1(w), b_4(w)$ and $b_6(w)$ are used. Negative initial history functions result in negative solutions which are presented with dashed lines. Specific parameter values are given below. $p = 2, \epsilon = .1, d_m = 1, a = 2, q = .5$ and $\tau = 0.5$.

Figure 2.3 represents a numerical verification of Theorem 7 when the birth functions $b_1(w), b_4(w)$ and $b_6(w)$ are used. We have similar results with the other birth functions (i.e. $b(w) = b_i(w)$ for $i = 2, 3, 5$). Note that the condition **H2** is not satisfied for b_4, b_5 and b_6. Nevertheless the numerical results suggest the global attractivity of the trivial solution when these birth functions are considered. This may indicate that condition **H2** can be too restrictive. Specific parameter values are $p = 2, \epsilon = .1, d_m = 1, a = 2, q = .5$ and $\tau = 0.5$. The next section deals with local stability of the steady states with respect to the wave equation.

2.6 Local analysis of the wave equation

In the following pages we will investigate the stability of steady state ϕ_j of (2.8) for all possible cases of α, c and $\tau \geq 0$.

Case 1: $\alpha = 0,\ c = 0,\ \tau \geq 0$

Lemma 4. Let $\alpha = 0$, $c = 0$. If $\epsilon b'(\phi_j) - d_m < 0 (> 0)$ then ϕ_j is a saddle (center) steady state of (2.8). In particular, if $b(\phi) = b_i(\phi)$, $i = 1, \ldots, 6$ and $\frac{\epsilon p}{d_m} > \max\{1, 4a\}$ then ϕ_1 for $i = 1, 2, 3$ and ϕ_2 for $i = 4, 5, 6$ are centers while ϕ_1 for $i = 4, 5, 6$, ϕ_2 for $i = 1, 2, 3$ and ϕ_3 for $i = 4, 6$ are saddles.

Proof.

When $\alpha = 0$ and $c = 0$ the characteristic equation (2.12) is reduced to

$$D_m \lambda^2 - d_m + \epsilon b'(\phi_j) = 0. \tag{2.50}$$

Define $A_j = \epsilon b_i'(\phi_j) - d_m$. Then considering non-degenerate cases, $(\phi_j, 0)$ is a saddle if $A_j < 0$ and ϕ_j is a center if $A_j > 0$. When $b(\phi) = b_i(\phi)$, $i = 1, \ldots, 6$, the result is obtained following the same procedure as given in proof of Lemma 2. □

Table 2.3: The parameter values used to obtain plots of the Figure 2.4

Plot	ϵ	d_m	D_m	p	a	q	K_c
Top left	1	1	1	6	1	1	-
Top right	1	1	1	6	1	1	-
Middle left	1	1	1	7	2	1	3
Middle right	1	1	1	7	2	-	-
Bottom left	1	2	1	8	3	-	-
Bottom right	2	2	1	8	1.7	-	-

Remark 7. Although equations (2.7) and (2.8) share the same steady states, the stability of each steady state is different with respect to each equation. Considering case 1, an unstable steady state ϕ_j of (2.7) is a center for the equation (2.8) while an asymptotically stable steady state of (2.7) becomes a saddle steady state of (2.8).

The numerical investigations are carried out with the computer package Matlab. Specifically, the toolbox "pplane7 " is employed to generate the phase-planes of the wave equation. The toolbox is freely available (http://math.rice.edu/$\sim$ dfield) for scientific research and it is provided by By Dr. John C. Polking, Department of Mathematics, Rice University, Houston, TX. Figure 2.4 represents the phase-plane of the wave equation (2.8) with the birth functions $b(\phi) = b_i(\phi)$, $i = 1, \ldots, 6$. Each plot represent the phase-plane corresponding to a certain birth function $b(\phi) = b_i(\phi), i = 1, \ldots, 6$. The parameter values used to obtain each plot are given in Table 2.3.

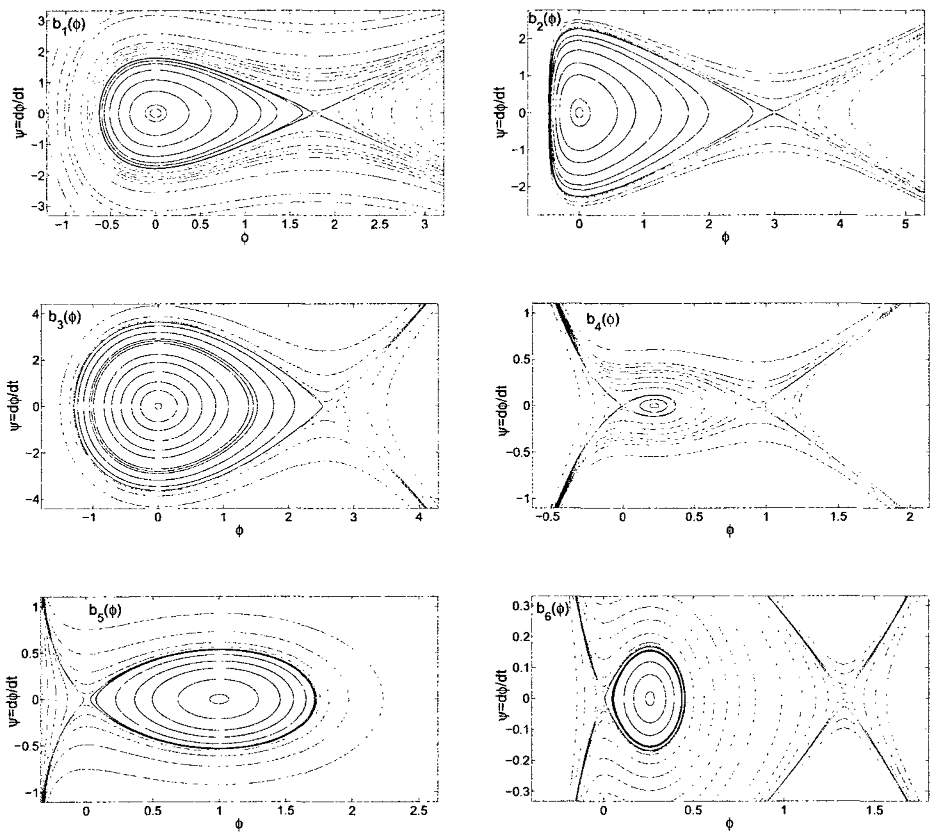


Figure 2.4: Phase-plane of the wave equation (2.8) when $\alpha = 0$ and $c = 0$. Each steady state is either a saddle or a center. From top left to bottom right plot, the birth functions $b_1(\phi) - b_6(\phi)$ are used. See Table 2.3 for the specific parameter values.

Case 2: $\alpha = 0$, $c > 0$, $\tau = 0$

The following Lemma indicates that in the absence of delay, any perturbation by wave speed c results in loss of center steady state.

Lemma 5. Let $\alpha = 0$, $c > 0$ and $\tau = 0$. Then all steady states of (2.8) are unstable. In particular, if $\epsilon b'(\phi_j) - d_m > 0$ then ϕ_j is an unstable node for $c > 2\sqrt{D_m(\epsilon b'(\phi_j) - d_m)}$ and an unstable spiral for any $c > 0$ smaller than that. if $\epsilon b'(\phi_j) - d_m < 0$ then ϕ_j is a saddle for any $c > 0$.

Proof.

When $\alpha, \tau = 0$, the characteristic equation (2.12) is reduced to

$$D_m\lambda^2 - c\lambda - d_m + \epsilon b^{'}(\phi_j) = 0. \tag{2.51}$$

Hence the eigenvalues are given by

$$\lambda_{\pm} = \frac{c \pm \sqrt{c^2 - 4D_m(\epsilon b^{'}(\phi_j) - d_m)}}{2D_m}. \tag{2.52}$$

Since $c > 0$; $Re(\lambda_+) > 0$ for all the cases. Depending on the sign of $\epsilon b^{'}(\phi_j) - d_m$ and the magnitude of $c > 0$, the possible cases for $\lambda_{\pm}$ give rise to each conclusion. $\square$

Remark 8. From Lemma 5 and the proof of Lemma 2, we have the following outcomes. If $b(\phi) = b_i(\phi)$, $i = 1, \ldots, 6$ then ϕ_1 for $i = 1, 2, 3$ and ϕ_2 for $i = 4, 5, 6$ are unstable nodes when c is sufficiently large, otherwise they are unstable spirals. Moreover ϕ_1 for $i = 4, 5, 6$, ϕ_2 for $i = 1, 2, 3$ and ϕ_3 for $i = 4, 6$ are saddle.

Remark 9. A major outcome of Lemma 5 is that any perturbation of c from zero results in loss of the periodic wave solutions and the homoclinc orbits corresponding to stationary wave pulses. We will discuss the disappearance of such solutions in Chapter 4.

Table 2.4: The parameter values used to obtain plots the Figures 2.5 and 2.6

Plot	c_1	c_2	ϵ	d_m	D_m	p	a	q	K_c
Top left	0.4	5	1	1	1	6	1	1	-
Top right	0.4	4	1	1	1	6	1	1	-
Middle left	0.5	5	1	1	1	7	2	1	3
Middle right	0.3	1.5	1	1	1	7	2	-	-
Bottom left	0.3	2	1	2	1	8	3	-	-
Bottom right	0.3	2	2	2	1	1	1.7	-	-

Note: Columns c_1 and c_2 are the values used for Figures 2.5 and 2.6 respectively.

The wavefront connecting steady state ϕ_1 to ϕ_2 can not be monotonic when ϕ_1 is a spiral. A necessary condition for monotonicity of the wavefront is that at least one of the eigenvalues corresponding to ϕ_1 must be a real positive value. If $\epsilon b'(\phi_1) - d_m > 0$ then by Lemma 5, ϕ_1 is not a spiral for $c > 2\sqrt{D_m(\epsilon b'(\phi_1) - d_m)}$. The value $c^* = 2\sqrt{D_m(\epsilon b'(\phi_1) - d_m)}$ is known as the minimal wave speed.

Remark 10. Let $b(\phi) = b_i(\phi)$ for $i = 1, 2, 3$, then the minimal speed c^* is given by $c^* = 2\sqrt{D_m(\epsilon b'(\phi_1) - d_m)}$.

Figures 2.5 and 2.6 represent the phase-plane of the wave equation (2.8) for the cases $c > 0$ small and large (i.e. $c > 2\sqrt{D_m(\epsilon b'(\phi_1) - d_m)}$) respectively. The parameter values used to obtain each plot of the Figures 2.5 and 2.6 are given in Table 2.4. For the Figures 2.5 and 2.6, the values of c are respectively given in the columns c_1 and c_2. All other parameter values are the same.

While cases 1 and 2 are straightforward we will see that the remaining cases demand sophisticated techniques to investigate the local stability of steady states.

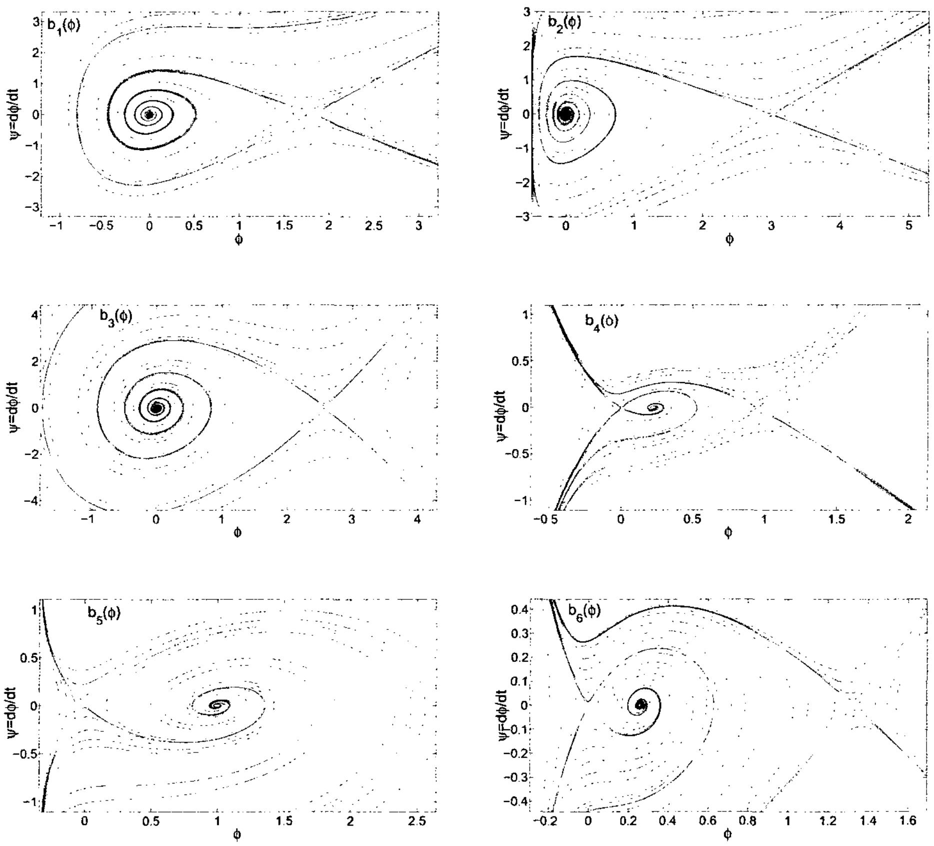


Figure 2.5: Phase-plane of the wave equation (2.8) when $\alpha = 0, \tau = 0$ and $c > 0$ is small. Comparing to the case $c = 0$ the center steady states have changes to unstable spirals. From top left to bottom right plot, the birth functions $b_1(\phi) - b_6(\phi)$ are used. The parameter values used to obtain each plot are given in Table 2.4.

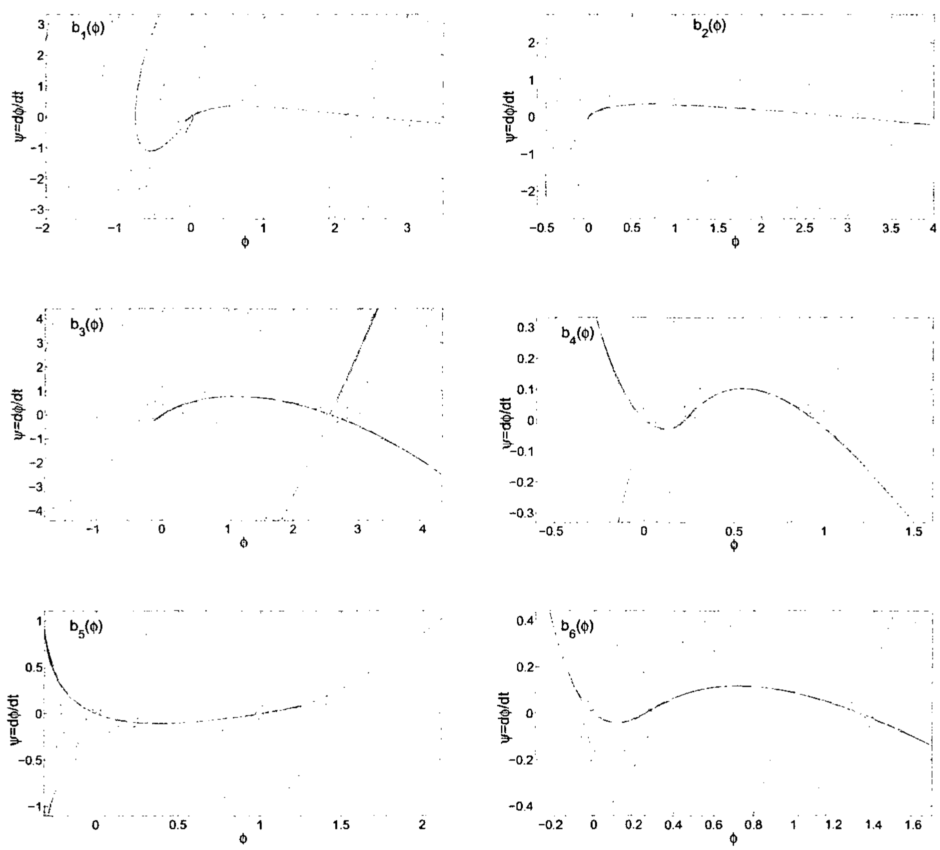


Figure 2.6: Phase-plane of the wave equation (2.8) when $\alpha = 0, \tau = 0$ and $c > 0$ is large. Comparing to the case $c = 0$ the center steady states have changed to unstable nodes. From top left to bottom right plot, the birth functions $b_1(\phi) - b_6(\phi)$ are used. The parameter values used to obtain each plot are given in Table 2.4.

<u>**Case 3:** $\alpha = 0,\ c > 0,\ \tau > 0$</u>

When $\alpha = 0$, the characteristic equation (2.12) is reduced to

$$D_m\lambda^2 - c\lambda - d_m + \epsilon b'(\phi_j)e^{-c\tau\lambda} = 0. \tag{2.53}$$

This can be rewritten as

$$e^{-c\tau\lambda} = a_0(\lambda - r_1)(\lambda - r_2), \tag{2.54}$$

where $a_0 = \frac{-1}{\epsilon b'(\phi_j)}$ and $r_{1,2} = \frac{c\pm\sqrt{c^2+4d_m D_m}}{2D_m}$.

As shown in [150], the solution of equation (2.54) is a function of λ with r_1, r_2 and a_0 as parameters. In particular, assume that there exists a value y such that the equation (2.54) is decomposed as

$$e^{-\frac{c\tau}{2}\lambda y} = a_0(\lambda - r_1), \tag{2.55}$$

$$e^{-\frac{c\tau}{2}\lambda(2-y)} = (\lambda - r_2). \tag{2.56}$$

Using Lambert W function, equations (2.55) and (2.56) have exact solutions $\lambda_1^{(y)}$ and $\lambda_2^{(y)}$ respectively. Then the problem of finding the solution λ of (2.54) is reduced to finding a value y such that $\lambda_1^{(y)}=\lambda_2^{(y)}$.

Let $y = 1 + \epsilon^*$, then it can be shown [150] that the solution λ of (2.54) is given by

$$\lambda = -\frac{1}{c\tau}\ln\left(\frac{4a_0W(z_1)W(z_2)}{(1+\epsilon^*)(1-\epsilon^*)(c\tau)^2}\right), \tag{2.57}$$

where ϵ^* is a function of a_0, r_1, r_2 and $c\tau$, W is the Lambert W function,

$$z_1 = (1+\epsilon^*)\frac{c\tau}{2a_0}e^{\frac{-r_1(1+\epsilon^*)c\tau}{2}}, \tag{2.58}$$

and

$$z_2 = (1-\epsilon^*)\frac{c\tau}{2}e^{\frac{-r_2(1-\epsilon^*)c\tau}{2}}. \tag{2.59}$$

Let η be the parameter in the series expansion of $\lambda_1^{(y)} - \lambda_2^{(y)}$. Then following the same procedure outlined in [150], the solution λ of (2.54) is given by

$$\lambda = -\frac{1}{c\tau}\ln\left(\frac{W(c\tau e^{-c\tau})}{(c\tau)}\right), \tag{2.60}$$

provided the following conditions hold.

1. **C1)** $|\epsilon^* - 1| < \delta$, with δ sufficiently small

2. **C2)** $\eta = \frac{1}{2} + \frac{W(c\tau e^{-c\tau})}{2c\tau}$.

In particular, we have the following proposition.

Proposition 1. Let $\alpha = 0$ and let the conditions **C1** and **C2** be satisfied. Then the steady state ϕ_j of the wave equation (2.8) is unstable.

Proof.

Following the properties of Lambert W function it can be shown that for $c\tau > 0$, $W(c\tau e^{-c\tau}) < c\tau$. Hence, from equation (2.60) we have that $\lambda > 0$. This completes the proof. □

Although under conditions **C1** and **C2** the steady state ϕ_j of (2.8) is unstable, these conditions are not practical. For instance, ϵ^* is a function of the parameters $D_m, c, \ldots$. But the function is not explicitly defined and we do not exactly know under what parameter changes $\epsilon^* \to 1$. To avoid such a problem we have the following proposition.

Proposition 2. Let $\alpha = 0$. If $\epsilon b'(\phi_j) - d_m < 0$, then for any $\tau \geq 0$, $c \geq 0$, ϕ_j is unstable.

Proof.

Define

$$f_0(\lambda) := D_m\lambda^2 - c\lambda - d_m + \epsilon b'(\phi_j)e^{-c\tau\lambda}. \tag{2.61}$$

Clearly when $\alpha = 0$, $f_0(\lambda) = 0$ represents the characteristic equation (2.53). Then we have $f_0(0) < 0$. Considering that $f_0(\lambda)$ is a continuous function of λ which eventually increases as λ increases. We get that $f_0(\lambda)$ has a real positive root. This completes the proof. □

Remark 11. Existence of a real positive root λ is the first step toward existence of a monotonic traveling wavefront. Specifically, the monotonic traveling wavefront can be seen as the heteroclinic path connecting two steady states of (2.8)

Remark 12. From Proposition 2 we get that when $b(\phi) = b_i(\phi)$, ϕ_1 for $i = 4, 5, 6$, ϕ_2 for $i = 1, 2, 3$ and ϕ_3 for $i = 4, 6$ are unstable steady states of (2.8).

Remark 13. Although Proposition 2 does not determine stability of all possible steady states when $b(\phi_j) = b_i(\phi_j)$, it shows that when $\alpha = 0$ at least one of the steady states of (2.8) is unstable.

The computation of characteristic roots is carried out with Matlab package TRACE-DDE. This is freely available for scientific research (see *http : //users. dimi.uniud.it/ ∼ dimitri.breda/software.html*). Details of this package are given as a book Chapter in [27]. Figure 2.7 represents the roots of characteristic equation (2.53) when $b(\phi) = b_i(\phi)$. Numerical explorations suggest that in all of the cases there exist at least one real positive root. This suggests instability of all steady states in the case that $\alpha = 0$, $c > 0$, $\tau > 0$. Note that when $\phi = \phi_1$ (i.e. the last Figure on the right hand side) the characteristic roots are the same for all $b(\phi) = b_i(\phi), i = 1 \ldots 6$.

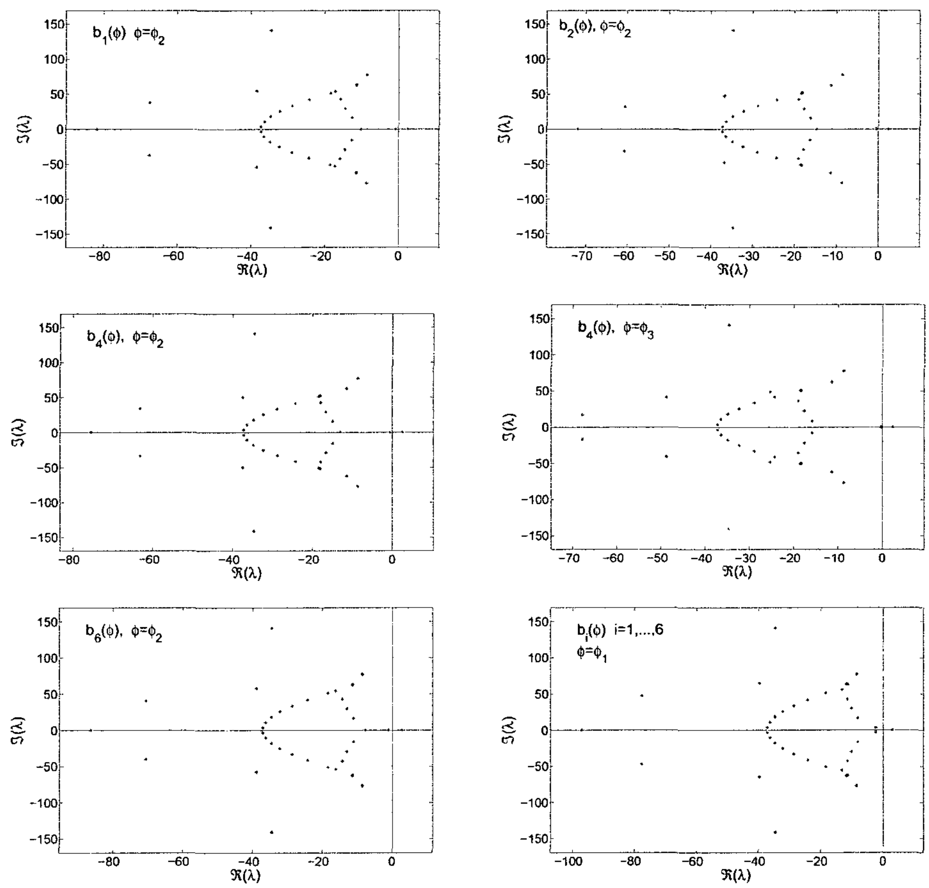


Figure 2.7: Plot of 42 characteristic roots on the complex plane, the parameter values are basically those of previous studies (e.g. [103]). Specifically, $\alpha = 0, d_m = 1, D_m = 1, p = 6, \epsilon = 1, a = 1, q = 1, c = 2, \tau = 0.25$. The birth function $b_i(\phi)$, $i = 1, \ldots, 6$ and the steady state ϕ_j used to obtain each graph have been specified in each plot.

Case 4: $\alpha > 0$, $c = 0$, $\tau \geq 0$

In this case the characteristic equation (2.12) is reduced to,

$$D_m\lambda^2 - d_m + \epsilon b_i'(\phi_j)e^{\alpha\lambda^2} = 0. \tag{2.62}$$

Let $z = \alpha\lambda^2$ then multiplying (2.62) by $\frac{\alpha}{D_m}$ we get that

$$z - \frac{\alpha d_m}{D_m} + \frac{\alpha\epsilon b_i'(\phi_j)}{D_m}e^z = 0. \tag{2.63}$$

Let $\tilde{z} = \frac{\alpha d_m}{D_m} - z$, then equation (2.63) is transformed into

$$\tilde{z}e^{\tilde{z}} = \frac{\alpha\epsilon b_i'(\phi_j)}{D_m}e^{\frac{\alpha d_m}{D_m}}. \tag{2.64}$$

The solution of (2.64) is given by the Lambert W function in the form of

$$\tilde{z} = W\left(\frac{\alpha\epsilon b_i'(\phi_j)}{D_m}e^{\frac{\alpha d_m}{D_m}}\right). \tag{2.65}$$

Hence, we get that

$$\lambda_\pm = \pm\sqrt{\frac{A_{ij}}{\alpha}}, \tag{2.66}$$

where

$$A_{ij} = \frac{\alpha d_m}{D_m} - W\left(\frac{\alpha\epsilon b_i'(\phi_j)}{D_m}\exp(\frac{\alpha d_m}{D_m})\right). \tag{2.67}$$

Note that the Lambert W function $W(x)$ is multivalued for $x \in (-e^{-1}, 0)$ and is not defined for $x < -e^{-1}$. Hence, it is required that $b'(\phi_j) > 0$. When $b(\phi_j) = b_i(\phi_j)$, this is equivalent to $\frac{\epsilon p}{d_m} < e^{1/q}$ for $i = 1$ and $\frac{\epsilon p}{d_m} < 1 + \frac{1}{q}$ for $i = 3$. Since $e^{\frac{1}{q}} > 1 + \frac{1}{q}$ we can combine these two conditions into $\frac{\epsilon p}{d_m} < 1 + \frac{1}{q}$. Moreover, for the case $i = 4$, $j = 3$ we need additional condition $\frac{\epsilon p}{d_m} < \frac{ae^2}{2}$. This is due to the fact that $b_4'(\phi) = pe^{-a\phi}\phi(2 - a\phi)$ is positive if $0 < \phi < \frac{2}{a}$. Considering that $\epsilon p\phi e^{-a\phi} = d_m$, we conclude the inequality before the last for ϕ_3. Note that $\phi_2 < \frac{1}{a}$ and therefore $b_4'(\phi_2) > 0$. In all other cases we have $b_i'(\phi_j) > 0$.

The following proposition deals with steady states of (2.8) for specific birth functions $b_i(\phi)$.

Proposition 3. In equation (2.8), let $\alpha > 0$ and $c = 0$. If $d_m > \epsilon b'(\phi_j)\exp(\frac{\alpha d_m}{D_m}) > \frac{D_m}{\alpha}$, then ϕ_j is a saddle. When both inequalities are reversed, ϕ_j is a center. In particular, when $b(\phi) = b_i(\phi)$, $i = 1, \ldots, 6$.

(i) If α is small enough or D_m is sufficiently large and $\frac{\epsilon p}{d_m} > 1$, then ϕ_1 for $i = 1, 2, 3$ is a center.

(ii) ϕ_1 for $i = 4, 5, 6$ is a saddle.

(iii) If $1 < \frac{\epsilon p}{d_m} < 1 + \frac{1}{q}$ and $\frac{\alpha\epsilon b_i'(\phi_2)}{D_m} > 1$ for $i = 1, 2, 3$, then for α small enough or D_m sufficiently large, ϕ_2 for $i = 1, 2, 3$ is a saddle.

(iv) ϕ_2 for $i = 4, 5, 6$ is a center if $\frac{\epsilon p}{d_m} > 4a$ and either α small enough or D_m sufficiently large.

(v) ϕ_3 for $i = 4, 6$ is a saddle if $\frac{\epsilon p}{d_m} > 4a$, $\frac{\alpha\epsilon b_i'(\phi_3)}{D_m} > 1$ and either α small enough or D_m sufficiently large.

Proof.

The eigenvalues of the linearized equation are given in (2.66) clearly when $A_{ij} > (<)0$, the steady state ϕ_j is a saddle (center). The Lambert W function has the following properties,

$$x - W(x) > 0, \text{ for } x > 1,$$

$$x - W(x) < 0, \text{ for } 0 < x < 1.$$

Hence

$$A_{ij} > (<)\frac{\alpha d_m}{D_m} - \frac{\alpha\epsilon b_i'(\phi_j)}{D_m}\exp(\frac{\alpha d_m}{D_m}), \tag{2.68}$$

when

$$\frac{\alpha\epsilon b_i'(\phi_j)}{D_m}\exp(\frac{\alpha d_m}{D_m}) > (<)1. \tag{2.69}$$

Noting that we should have $A_{ij} > (<)0$, from (2.68) and (2.68) we get that ϕ_j is a saddle (center) when

$$d_m > (<)\epsilon b_i'(\phi_j)\exp(\frac{\alpha d_m}{D_m}) > (<)\frac{D_m}{\alpha}. \tag{2.70}$$

Case i

For $i = 1, 2, 3$, $b_i'(\phi_1) = p$. Since $\epsilon p > d_m$, we have $d_m < \epsilon b_i'(\phi_1)\exp(\frac{\alpha d_m}{D_m})$. Also $\epsilon b_i'(\phi_1)\exp(\frac{\alpha d_m}{D_m}) < \frac{D_m}{\alpha}$, when α is small enough or D_m is large.

Case ii

For $i = 4, 5, 6$, $b_i'(\phi_1) = 0$. From (2.67) we get that

$$A_{i1} = \frac{\alpha d_m}{D_m} > 0.$$

Case iii

The condition $\frac{\epsilon p}{d_m} < 1 + \frac{1}{q}$ guarantees that $b_i'(\phi_2) > 0$. Since $\frac{\alpha \epsilon b_i'(\phi_2)}{D_m} > 1$ for $i = 1, 2, 3$, the term in (2.69) is greater than 1 and therefore A_{i2} in D_m is greater than the righthand side. As shown in the proof of Lemma 2, $\frac{\epsilon p}{d_m} > 1$ implies that $\epsilon b_i'(\phi_2) - d_m < 0$. Hence for α small enough or D_m sufficiently large we have,

$$\frac{\alpha}{D_m}\left(d_m - \epsilon b_i'(\phi_j)\exp(\frac{\alpha d_m}{D_m})\right) \geq 0,$$

for $i = 1, 2, 3$, which implies the conclusion.

Case iv

The condition $\frac{\epsilon p}{d_m} > 4a$ guarantees existence of ϕ_2 for $i = 4, 5, 6$. Choosing α sufficiently small or D_m sufficiently large enough the term in (2.69) is less than 1. Then we get that the righthand side of (2.68) is greater than A_{i2}. As shown in the proof of Lemma 2 we have $\epsilon b_i'(\phi_2) - d_m > 0$ for $i = 4, 5, 6$, which immediately results in $A_{i2} < 0$. This completes the proof. □

Case v

The Proof is similar to Case iii. □

Remark 14. When $\alpha > 0$, Proposition 3 indicates that the phase-plane of the wave equation (2.8) can qualitatively remain the same as the case $\alpha = 0$ (see Lemma 4). This has been numerically confirmed. In particular when the conditions of Proposition 3 are satisfied, phase-planes are quite similar to those of Figure 2.4.

Case 5: $\alpha > 0,\ c > 0,\ \tau \geq 0$

When all parameters α, c and τ are positive, finding the roots of the characteristic equation is a nontrivial task. However, an algebraic approach to the problem of finding real roots of (2.12) indicates useful facts.

Define,

$$f(\lambda) := \epsilon b_i'(\phi_j)e^{\alpha\lambda^2 - c\tau\lambda}, \tag{2.71}$$

$$g(\lambda) := -D_m\lambda^2 + c\lambda + d_m. \tag{2.72}$$

Then the characteristic equation (2.12) is given by

$$f(\lambda) = g(\lambda). \tag{2.73}$$

Assume that $b'(\phi_j) > 0$. One can simply observe that for $\lambda \in \mathbb{R}$, $g(\lambda)$ reaches its only maximum at

$$(\lambda_M, g_M) = (\frac{c}{2D_m}, \frac{c^2}{4D_m + d_m}), \tag{2.74}$$

and $f(\lambda)$ reaches its only minimum at

$$(\lambda_m, f_m) = (\frac{c\tau}{2\alpha}, \epsilon b_i'(\phi_j)\exp(c^2(\frac{\alpha}{4D_m^2} - \frac{\tau}{2\alpha}))). \tag{2.75}$$

The characteristic equation (2.12) admits a positive real root λ_r when $f(\lambda)$ and $g(\lambda)$ are tangent or intersect at λ_r. Figure 2.8 demonstrates such a case. When $\tau = \frac{\alpha}{D_m}$ the maximum point of $g(\lambda)$ is the same as minimum point of $f(\lambda)$ (i.e. $\frac{c}{2D_m} = \frac{c\tau}{2\alpha}$). The following Lemma shows that under such conditions the real roots of (2.8) can be calculated by means of the Lambert W function. Moreover, stability of ϕ_j is determined.

Lemma 6. Let $\alpha > 0$, $c > 0$, $\tau = \frac{\alpha}{D_m}$. If $b'(\phi_j) > 0$, then the steady state ϕ_j is unstable. Furthermore, the characteristic equation (2.12) has exact solutions,

$$\lambda_{\pm} = \frac{c\tau \pm \sqrt{(c\tau)^2 + 4\alpha A_{ij}}}{2\alpha}.$$

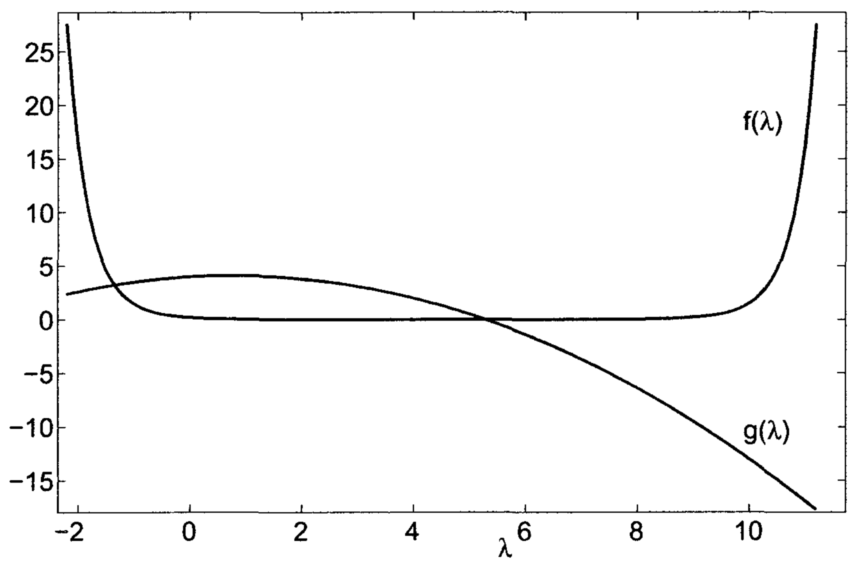


Figure 2.8: plot of $f(\lambda)$ and $g(\lambda)$. For $\lambda \in \mathbb{R}$, when $b'(\phi_j) > 0$ and $g_M \geq f_m$, f and g intersect at some $\lambda_r > 0$, which is a real positive eigenvalue of (2.8). See Lemma 6 for more details.

Proof.

Multiplying the equation (2.12) by $\frac{\alpha}{D_m}$, including the terms $\pm c\tau\lambda$ and considering that $c(\tau - \frac{\alpha}{D_m}) = 0$ we get that,

$$z - \frac{\alpha d_m}{D_m} + \frac{\alpha \epsilon b_i'(\phi_j)}{D_m} e^z = 0, \tag{2.76}$$

where

$$z = \alpha\lambda^2 - c\tau\lambda. \tag{2.77}$$

Let $\tilde{z} = \frac{\alpha d_m}{D_m} - z$, then equation (2.76) is transformed into

$$\tilde{z}e^{\tilde{z}} = \frac{\alpha\epsilon b_i'(\phi_j)}{D_m} e^{\frac{\alpha d_m}{D_m}}. \tag{2.78}$$

Using Lambert W function we get that $z = A_{ij}$, where A_{ij} is defined in (2.67). Then substituting $z = A_{ij}$ into (2.77) and solving for λ, we have the roots $\lambda_{\pm}$. Obviously $Re(\lambda_+) > 0$ for $c > 0$. Hence ϕ_j $j = 1, 2, 3$ is unstable. □

Remark 15. When $b(\phi) = b_i(\phi)$, the condition $b_i'(\phi_j) > 0$ for $i = 1, \ldots, 6$ and $j = 2, 3$ is equivalent to $\frac{\epsilon p}{d_m} < 1 + \frac{1}{q}$ for the cases $i = 1, 3$ and $j = 2$. It is also equivalent to $\frac{\epsilon p}{d_m} < \frac{ae^2}{2}$ for $i = 4$, $j = 3$. In all other cases the condition $b_i'(\phi_j) > 0$ is already satisfied

But what can be said when $\tau \neq \frac{\alpha}{D_m}$? In the following we shall establish the instability conditions for the steady state ϕ_j when $0 < c \ll 1$ or $\left|\tau - \frac{\alpha}{D_m}\right| \ll 1$. Let

$$f_z(\lambda) := z + \frac{\epsilon b_i'(\phi_j)\alpha}{D_m} e^z - \frac{\alpha d_m}{D_m},$$

where $z = \alpha\lambda^2 - c\tau\lambda$. Let

$$g_\tau(\lambda) := c(\tau - \frac{\alpha}{D_m})\lambda.$$

Then the characteristic equation (2.12) is written as

$$f_z(\lambda) + g_\tau(\lambda) = 0. \tag{2.79}$$

The following theorem is due to French mathematician Eugene Rouche (1832-1910).

Theorem 8 (Rouche). If $f(z)$ and $g(z)$ are analytic inside and on a simple closed curve C and if $|g(z)| < |f(z)|$ on C, then $f(z)+g(z)$ and $f(z)$ have the same number of zeros inside C.

Proof.

The proof is given on page 128 of [168]. □

Using Rouche's Theorem and Lemma 6 we have the following Theorem.

Theorem 9. Let $\alpha > 0$ and $c > 0$. Let $b'(\phi_j) > 0$. If c or $\left|\tau - \frac{\alpha}{D_m}\right|$ is sufficiently small, then the steady state ϕ_j of (2.8) is unstable.

Proof.

By Lemma 6, $f_z(\lambda) = 0$ has the roots λ_+ and λ_-. Let $0 < r < Re(\lambda_+)$; Let $B(\lambda_+, r)$ be the circle centered at λ_+ with radius r; then the maximum value of $|g_\tau(\lambda)|$ on the circle $B(\lambda_+, r)$ is obtained as follows. Let $\lambda \in B(\lambda_+, r)$ then $\lambda = \lambda_+ + re^{i\theta}$ for some $0 \le \theta < 2\pi$. We have

$$\begin{aligned}
|g_\tau(\lambda)| &= \left|c(\tau - \tfrac{\alpha}{D_m})\right| \left|\lambda_+ + re^{i\theta}\right|, \\
&= \left|c(\tau - \tfrac{\alpha}{D_m})\right| ((Re(\lambda_+) + r\cos\theta)^2 + (Im(\lambda_+) + r\sin\theta)^2)^{1/2}, \\
&= \left|c(\tau - \tfrac{\alpha}{D_m})\right| (|\lambda_+|^2 + r^2 + 2rRe\lambda_+ \cos\theta + 2rIm(\lambda_+)\sin\theta)^2)^{1/2}.
\end{aligned}$$

Using the trigonometric equality,

$$\alpha \sin\theta + b\cos\theta = \sqrt{a^2+b^2}\sin(\theta + \varphi),$$

with $\varphi = \sin^{-1}(\frac{b}{\sqrt{a^2+b^2}})$ we have,

$$\sigma = \max_{0<\theta\le 2\pi} |g_\tau(\lambda)| = \left|c(\tau - \frac{\alpha}{D_m})\right| (|\lambda_+| + r). \tag{2.80}$$

Define the two variable function $h : \mathbb{R}^2 \to \mathbb{R}$ as $h(x,y) = |f_z(x+iy)|^2$.

Claim: $(Re\lambda_+, Im\lambda_+)$ is a local minimum of the function h.

Let $f_1 = Re(f(\lambda))$ and $f_2 = Imf(\lambda)$, then the gradient of h is given by,

$$\nabla h = \begin{bmatrix} h_x \\ h_y \end{bmatrix} = 2 \begin{bmatrix} f_1 f_{1x} + f_2 f_{2x} \\ f_1 f_{1y} + f_2 f_{2y} \end{bmatrix} \tag{2.81}$$

Since $f(\lambda_+) = 0$, we get that $f_i(\lambda_+) = 0$ for $i = 1, 2$. Hence $\nabla h(Re\lambda_+, Im\lambda_+) = 0$. Moreover,

$$\begin{aligned} h_{xx}(Re\lambda_+, Im\lambda_+) &= f_{1x}(\lambda_+)^2 + f_{2x}(\lambda_+)^2 \\ h_{yy}(Re\lambda_+, Im\lambda_+) &= f_{1yx}(\lambda_+)^2 + f_{2y}(\lambda_+)^2 \\ h_{xy}(Re\lambda_+, Im\lambda_+) &= f_{1x}(\lambda_+) f_{1y}(\lambda_+) + f_{2x}(\lambda_+) f_{2y}(\lambda_+). \end{aligned} \tag{2.82}$$

Define

$$D_h := det \begin{bmatrix} h_{xx} & h_{yx} \\ h_{xy} & h_{yy} \end{bmatrix} \tag{2.83}$$

Then

$$D_h(Re\lambda_+, Im\lambda_+) = (f_{1x}(\lambda_+) f_{2y}(\lambda_+) - f_{2x}(\lambda_+) f_{1y}(\lambda_+))^2 \tag{2.84}$$

Employing the second derivative test, (2.82) and (2.84) imply that $(Re\lambda_+, Im\lambda_+)$ is a local minimum for function h. Consequently, λ_+ is a local minimum for $|f(\lambda)|$. Choosing $r > 0$ small enough, $|f(\lambda)| > 0$ for all $\lambda \in B(\lambda_+, r)$. Hence,

$$\delta = \min_{0 < \theta \leq 2\pi} |f(\lambda)| > 0$$

and for τ, α, D_m fixed and c sufficiently small (or similarly for $c > 0$ fixed and $\left|\tau - \frac{\alpha}{D_m}\right|$ sufficiently small), $\delta > \sigma > 0$.

By Rouche's Theorem we conclude that the characteristic equation (2.79) has a root $\tilde{\lambda}$ such that $\tilde{\lambda}$ lies inside $B(\lambda_+, r)$. Since $0 < r < Re(\lambda_+)$, we see that $Re(\tilde{\lambda}) > 0$. This completes the proof. $\square$

Remark 16. As mentioned before, when $b(\phi) = b_i(\phi)$, conditions $\frac{\epsilon p}{d_m} < e^{\frac{1}{q}}$ for $i = 1$, $j = 2$, $\frac{\epsilon p}{d_m} < 1 + \frac{1}{q}$ for $i = 3$, $j = 2$ and $\frac{\epsilon p}{d_m} < ae^2$ for $i = 4$, $j = 3$ are to ensure that $b_i'(\phi_2) > 0$ for $i = 1$ and 3.

The following Theorem treats the problem in a more general fashion and it shows that the statement is true even though $b_i'(\phi_j) \leq 0$.

Theorem 10. In equation (2.8), let $\alpha > 0$. If c or $\left|\tau - \frac{\alpha}{D_m}\right|$ is sufficiently small, then the steady state ϕ_j of equation (2.8) is unstable.

Proof.

We only need to show this for $b_i'(\phi_j) \leq 0$, otherwise have the same as Theorem 9. Let $\lambda = u + iv$ be a root of (2.12), then equating the real and imaginary part of (2.53) to zero, we get that

$$D_m(u^2 - v^2) - cu - d_m + \epsilon b_i'(\phi_j)e^{\xi} \cos \eta = 0, \tag{2.85}$$

$$(2D_m u - c)v + \epsilon b_i'(\phi_j)e^{\xi} \sin \eta = 0, \tag{2.86}$$

where

$$\xi = -c\tau u + \alpha(u^2 - v^2), \tag{2.87}$$

$$\eta = v(2\alpha u - c\tau). \tag{2.88}$$

Let $\eta = 2k\pi$ for $k \in \mathbb{Z}\setminus\{0\}$, then from equation (2.86) we get that $u = \frac{c}{2D_m}$. Define the function f_τ as

$$f_\tau(v) := D_m v^2 - \frac{c^2}{4D_m} - d_m + \epsilon b_i'(\phi_j)\exp\left(\frac{c^2}{2D_m}\left(\frac{\alpha}{2D_m} - \tau\right) - \alpha v^2\right). \tag{2.89}$$

Substituting $\eta = 2k\pi$ and $u = \frac{c}{2D_m}$ we get that equation (2.85) is reduced to $f_\tau(v) = 0$. we have $b_i'(\phi_j) \leq 0$, therefore $f_\tau(0) < 0$. Substituting $u = \frac{c}{2D_m}$ into

(2.88) and solving $\eta = 2k\pi$ for v we get,

$$v = \frac{2k\pi}{c(\frac{\alpha}{D_m} - \tau)}. \tag{2.90}$$

Hence, v is described as a function of c and τ. When c decreases or τ approaches to $\frac{\alpha}{D_m}$, the magnitude of v increases. Considering equation (2.89), one can observe that $f_\tau(v)$ is an increasing function of the magnitude of v. Hence, there exists $c_n > 0$ (or equivalently there exists τ_n in a small neighborhood of $\frac{\alpha}{D_m}$) with $v_n = \frac{2k\pi}{c_n(\frac{\alpha}{D_m}-\tau)}$ such that $f_\tau(v_n) > 0$. By continuity of f_τ with respect to v we get that f_τ has a root $v_r \in (0, v_n)$ and $f_\tau(\pm v_r) = 0$. Hence, $\lambda = \frac{c}{2D_m} \pm iv_r$ are the eigenvalues of (2.8). Since $Re(\lambda) = \frac{c}{2D_m} > 0$, ϕ_j is unstable when $b_i'(\phi_j) \leq 0$. Otherwise, ϕ_j is unstable by Theorem 9. □

Table (2.5) is a summary of possible conditions for stability or instability of ϕ_j of equation (2.8). Concerning the asymptotic stability of ϕ_1, ϕ_2 or ϕ_3, in Table (2.5), we note that in none of the cases do we have asymptotic stability. So the main question is whether there is a case that ϕ_j is asymptotically stable. This is important since it is a necessary condition for existence of monotonic traveling wavefronts. In other words, if $\phi(t)$ is a monotone traveling wavefront of the RD equation (2.7), then we should have $\lim_{t\to-\infty} \phi(t) = \phi_1$ and $\lim_{t\to\infty} \phi(t) = \phi_2$ where ϕ_1 and ϕ_2 are respectively unstable and asymptotically stable steady states of (2.8). Let $\lambda = u + iv$ be an eigenvalue of ϕ_j corresponding to (2.8). Let $v \in \mathbb{R}$ be fixed. Define $r_v(u)$ and $s_v(u)$ as follows,

$$r_v(w) := (D_m(u^2 - v^2) - cu - d_m)^2 + (2D_m u - c)^2 v^2, \tag{2.91}$$

$$s_v(w) := \epsilon^2 b'^2(\phi_j) \exp(2\alpha(u^2 - v^2) - 2c\tau u). \tag{2.92}$$

From (2.85) and (2.86) we get that u must satisfy

$$r_v(u) = s_v(u). \tag{2.93}$$

Table 2.5: Stability of homogeneous steady states ϕ_j of (2.8)

α	c	τ	i for b_i	conditions	ϕ_1	ϕ_2	ϕ_3
0	0	0,+	$i = 1, 2, 3$	$\epsilon p/d_m > 1$	center	saddle	–
0	0	0,+	$i = 4, 5, 6$	$\epsilon p/d_m > 4a$	saddle	center	saddle
0	+	0	$i = 1, 2, 3$	$\epsilon p/d_m > 1$ c small	U spiral	saddle	–
0	+	0	$i = 4, 5, 6$	$\epsilon p/d_m > 1$ c small	saddle	U spiral	saddle
0	+	0	$i = 1, 2, 3$	$\epsilon p/d_m > 4a$ c large	U node	saddle	–
0	+	0	$i = 4, 5, 6$	$\epsilon p/d_m > 4a$ c large	saddle	U node	saddle
0	+	+	$i = 1, \ldots, 6$	$\epsilon^* \to 1, \eta = \frac{1}{2} + \frac{W(c\tau e^{-c\tau})}{2c\tau}$	U	U	U
0	0,+	0,+	$i = 1, 2, 3$	$\epsilon p/d_m > 1$	–	U	–
0	0,+	0,+	$i = 4, 5, 6$	$\epsilon p/d_m > 4a$	U	–	U
+	0	0,+	$i = 1, 2, 3$	$\epsilon p/d_m > 1, \alpha$ small or D_m large	center	–	–
+	0	0,+	$i = 1, 2, 3$	$\epsilon p/d_m > 1$	saddle	–	–
+	0	0,+	$i = 4, 5, 6$	$\epsilon p/d_m > 4a$	–	center	–
+	0	0,+	$i = 1, 2, 3$	$\epsilon 1 + 1/q > p/d_m > 1(4a)$	–	saddle	(saddle)
			$(i = 4, 6)$	$\alpha\epsilon b_i' > D_m\alpha$ small or D_m large			
+	+	+	$i = 1, 2, 3$	$\tau = \alpha/D_m, 1 + 1/q > \epsilon p/d_m > 1$	U	U	–
+	+	+	$i = 4$	$\tau = \alpha/D_m, ae^2 > \epsilon p/d_m > ae$	U	U	U
+	+	+	$i = 5, 6$	$\tau = \alpha/D_m, \epsilon p/d_m > 4a$	U	U	U

Note: U= unstable; in the last three cases the condition $\tau = \alpha/D_m$ can be replaced with $\left|\tau - \frac{\alpha}{D_m}\right|$ or $c > 0$ sufficiently small.

Taking the derivative of r_v and s_v we have

$$\frac{dr_v}{du} = 2(2D_m u - c)(D_m(u^2 + v^2) - cu - d_m), \tag{2.94}$$

$$\frac{ds_v}{du} = 2\epsilon^2 b'^2(\phi_j)(2\alpha u - c\tau)\exp(2\alpha(u^2 - v^2) - 2c\tau u). \tag{2.95}$$

Hence, $u = \frac{c\tau}{2\alpha}$ is the only local minimum of s_v. Taking the second derivative of s_v we get that

$$u = \frac{c\tau + \sqrt{c\tau}}{2\alpha},$$

are the inflection points of s_v. Furthermore, r_v may have either a local minimum at $u = \frac{c}{2D_m}$ or a local maximum at $u = \frac{c}{2D_m}$ and two local minimum at r_1 and r_2 that are the roots of the second term in (2.94). These are presented in Figure 2.9.

We are looking for a case that r_v and s_v only intersect at $u < 0$. This guarantees ϕ_j being asymptotically stable. Calculating the minimum values of r_v at r_1 and r_2 we get that they are of the same value. Specifically,

$$r_v(r_1) = r_v(r_2) = 4v^4 D_m^2(1 + c^2 - 4D_m(D_m v^2 - d_m)).$$

Moreover,

$$r_v(\frac{c}{2D_m}) = (\frac{c^2}{4D_m} - v^2 - d_m)^2.$$

Observe that the function $r_v(u)$ is symmetric with respect to the line $u = \frac{c}{2D_m}$. Similarly, the function $s_v(u)$ is symmetric with respect to the line $u = \frac{c\tau}{2\alpha}$. Let $\frac{c}{2D_m} \leq \frac{c\tau}{2\alpha}$. Suppose that r_v and s_v intersect at $u_- < 0$, then by symmetry of r_v and s_v, they must intersect at some u_+ with $0 < u_+ \leq |u_-|$. We conclude that when $\frac{c}{2D_m} \leq \frac{c\tau}{2\alpha}$ steady state ϕ_j is unstable. The following proposition states the conditions for existence of asymptotically stable steady state ϕ_j.

Proposition 4. Let $v \in \mathbb{R}$ be fixed. Let $r_v(0) < s_v(0)$ and $(\frac{c^2}{4D_m} - v^2 d_m)^2 < \epsilon^2 b_i'^2(\phi_j)$ if $\frac{1}{D_m} > \frac{\tau}{\alpha}$ and $\left|\frac{\tau}{\alpha} - \frac{1}{D_m}\right|$ is sufficiently large then ϕ_j of (2.8) is asymptotically stable.

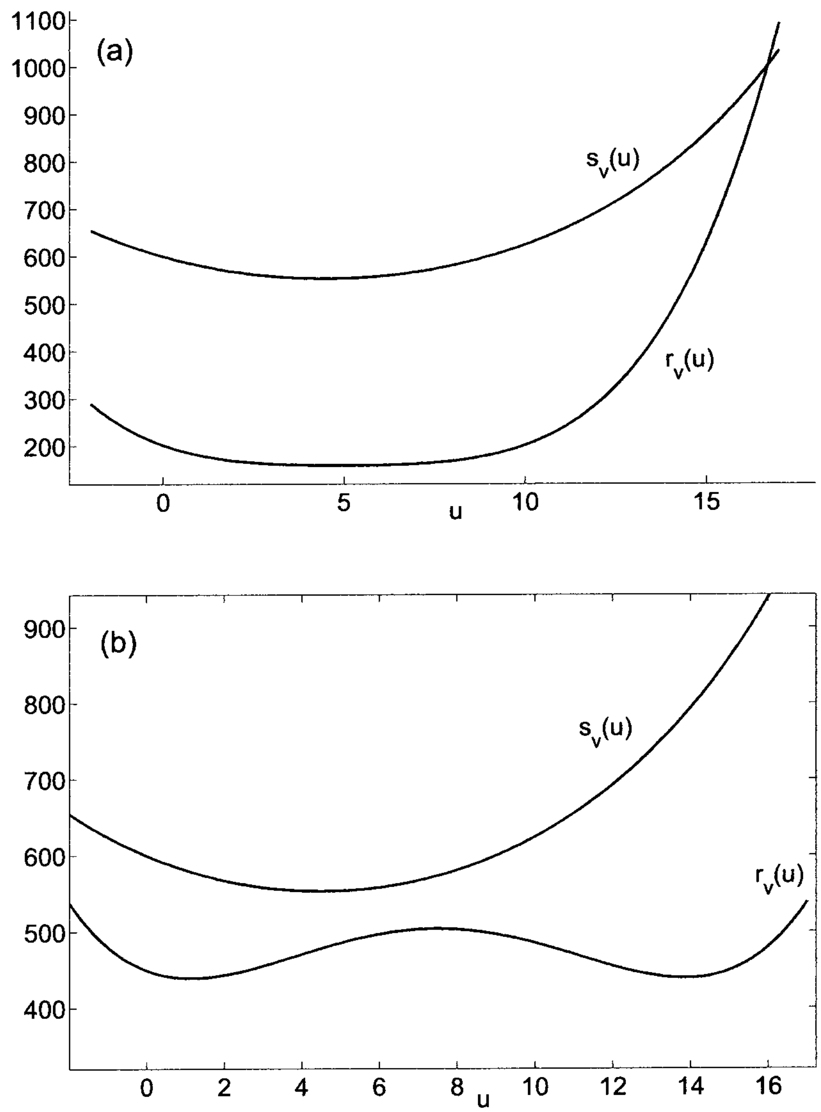


Figure 2.9: a) and b) Graph of $r_v(u)$and $s_v(u)$ for two possible cases, see the text for more details.

Proof.

Let $\lambda = u + iv$ be the eigenvalue corresponding to the characteristic equation (2.12). Choosing $\left|\frac{\tau}{\alpha} - \frac{1}{D_m}\right|$ sufficiently large, By the symmetry of r_v and s_v, there exists $u < 0$ that satisfies (2.93). From $r_v(0) < s_v(0)$ we get that $r_v(\frac{c}{D_m}) < s_v(\frac{c\tau}{\alpha})$. Observe that s_v increases exponentially for $u > \frac{c\tau}{2\alpha}$ while r_v increases with degree 4 when $u > \frac{c}{2D_m}$. Also the condition $(\frac{c^2}{4D_m} - v^2 d_m)^2 < \epsilon^2 b_i'^2(\phi_j)$ guarantees that

$$\max_{0<u<c/D_m} r_v(u) < \min_u s_v(u).$$

We conclude that s_v and r_v do not intersect for any $u \geq 0$. □

Now that the existence of stable ϕ_j of (2.8) is established we are concerned with possible destabilizing effects of delay on the stability of ϕ_j. In particular let ϕ_j be stable when $c > 0$ and $\alpha, \tau \geq 0$. Then what will happen when τ is slightly perturbed? We have previously shown (Theorem 3) that under some conditions delay has no effect on the stability of homogeneous steady states of (2.7). However, this is not the case when wave equation (2.8) is considered. In the characteristic equation (2.12), we may consider the root $\lambda = \lambda(\tau)$ as a continuous function of τ. Then supposing that $Re(\lambda) \neq 0$ small changes to $\tau > 0$ do not affect the sign of $Re(\lambda)$. Furthermore, when $c > 0$ and $\tau = 0$, there exists no steady state with eigenvalue $Re(\lambda) = 0$. This can be seen by substituting $\lambda = iv$, $v \neq 0$ into equation (2.12). Then equating the imaginary part to zero, we get that $-cv = 0$, which is a contradiction. However, if $c > 0$ and $\tau > 0$ then substituting $\lambda = iv$ into (2.12) gives rise to

$$-D_m v^2 - d_m + \epsilon b'(\phi_j) e^{-\alpha v^2} \cos c\tau v = 0, \tag{2.96}$$

$$cv + \epsilon b'(\phi_j) e^{-\alpha v^2} \sin c\tau v = 0, \tag{2.97}$$

Moving the exponential terms in (2.96) and (2.97) to the other side, squaring them and adding them together we obtain,

$$(D_m v^2 + d_m)^2 + c^2 v^2 = \epsilon^2 b_i'^2(\phi_j) e^{-\alpha v^2}. \tag{2.98}$$

The following Theorem is concerned with loss of stability of steady state ϕ_j of (2.8).

Proposition 5. Let $c, \tau > 0$ and let $d_m < \epsilon \left|b_i'(\phi_j)\right|$ then the stable steady state ϕ_j of (2.8) loses its stability when τ is increased.

Proof.

Define the function $S(v)$ as

$$S(v) = (D_m v^2 + d_m)^2 + c^2 v^2 - \epsilon^2 b_i'^2(\phi_j) e^{-\alpha v^2}. \tag{2.99}$$

Clearly $S(v) = 0$ represents equation (2.98). Then condition $d_m < \epsilon \left|b'(\phi_j)\right|$ implies that $S(0) < 0$. By continuity of $S(v)$ with respect to v and the fact that $S(v)$ is an increasing function, there exists a positive real root v_r for (2.98). Hence, the pure imaginary root $\lambda = iv$ of (2.12) exists. Considering λ as a function of τ and taking the derivative of (2.12) with respect to τ we get that

$$(2D_m\lambda - c + \epsilon b'(\phi_j) e^{\alpha\lambda^2 - c\tau}(2\alpha\lambda - c\tau\lambda))\frac{d\lambda}{d\tau} = c\epsilon b'(\phi_j)\lambda e^{\alpha\lambda^2 - c\tau\lambda}. \tag{2.100}$$

From equation (2.12) we have

$$\epsilon b'(\phi_j) e^{\alpha\lambda^2 - c\tau\lambda} = -D_m\lambda^2 + c\lambda + d_m. \tag{2.101}$$

From (2.100) and (2.101) we get that

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{2D_m\lambda - c}{-D_m\lambda^2 + c\lambda + d_m} + \frac{2\alpha}{c} - \frac{\tau}{\lambda}. \tag{2.102}$$

Then evaluating $\frac{dRe(\lambda)}{d\tau}$ at $\lambda = iv$ we get that

$$\begin{aligned} \frac{dRe(\lambda)}{d\tau}(iv) &= Re\left(\frac{2D_m vi - c}{D_m\lambda^2 + d_m + cvi}\right) + \frac{2\alpha}{c}, \\ &= \frac{c(D_m v^2 + d_m)}{(D_m v^2 + d_m)^2 + c^2 v^2} + \frac{2\alpha}{c}. \end{aligned}$$

Hence, $\frac{dRe(\lambda)}{d\tau}(iv) > 0$. This implies that as τ increases, the roots of the form $\lambda = iv$ of (2.12) cross the imaginary axis from left to right. This completes the proof. $\square$

In summary, this chapter is concerned with the local stability of the steady states for all possible cases of $c, \tau, \alpha \geq 0$. The results of this chapter are crucial in studies of the traveling and stationary wave solutions of the model and they will be used in the forthcoming chapters.

Chapter 3

Stationary wave solutions

The main goal of the present chapter is to investigate the stationary wave solutions of the population model. In particular, when the wave solution of the population model (2.7) is stationary (i.e. $c = 0$), the corresponding wave equation is reduced to a delay independent second order differential equation. This allows us to take advantage of the well-established theory of ODEs to study the behavior of the stationary wave solutions. This chapter is organized as follows. Section 3.1 deals with global analysis of stationary waves, where by employing the Morse Lemma, the wave solutions can be locally approximated. In Section 3.2 conditions for existence and nonexistence of periodic stationary waves are discussed. In Section 3.3 stationary wave pulses of the model are obtained when specific birth functions are utilized. This work is followed by Section 3.4 where stationary wavefronts are obtained via the method of energy functions.

3.1 Preliminaries: global analysis of stationary waves

The main purpose of the section is to apply methods well-known in the study of nonlinear planar systems to study the local and global behavior of orbits (i.e. trajectories) of the wave equation in the phase-plane. We begin with some basic definitions.

Definition 2. *A system $\dot{x} = X(x,y)$, $\dot{y} = Y(x,y)$ is called a Hamiltonian system if there exists a function $H(x,y)$ such that $X = \frac{\partial H}{\partial y}$ and $Y = -\frac{\partial H}{\partial x}$. Then H is called the Hamiltonian function.*

Definition 3. *The orbital derivative of a differentiable function $F := \mathbb{R}^n \to \mathbb{R}$ along the vector function $x := \mathbb{R} \to \mathbb{R}^n$, parameterized by t is defined as*

$$L_t F = \frac{\partial F}{\partial x}\dot{x} = \frac{\partial F}{\partial x_1}\dot{x}_1 + \frac{\partial F}{\partial x_2}\dot{x}_2 + \ldots + \frac{\partial F}{\partial x_n}\dot{x}_n$$

Definition 4. *The function $F(x)$ is called first integral of the equation $\dot{x} = f(x)$, $x \in D \subset \mathbb{R}^n$ if $F(x)$ in D holds $L_t F = 0$, with respect to vector function $x(t)$.*

The first integral $F(x)$ is sometimes called the constants of motion. The reason for such a name is that $F(x)$ is constant along a solution $x(t)$. This can be seen from $L_t F = 0$. We may note that a Hamiltonian system always has a first integral. In fact the Hamiltonian function $H(x,y)$ is the first integral.

When $c = 0$ and $\alpha = 0$, the stationary wave equation of the population model (2.7) is given by

$$D_m \phi'' - d_m \phi + \epsilon b(\phi) = 0, \tag{3.1}$$

which is delay independent. Then equation (3.1) can be written as a conservative system of first order ODEs

$$\begin{cases} \frac{d\phi}{dt} = & \varphi \\ \frac{d\varphi}{dt} = & h_i(\phi), \end{cases} \tag{3.2}$$

where

$$h_i(\phi) = \frac{1}{D_m}(d_m\phi - \epsilon b(\phi)). \tag{3.3}$$

It can be verified that (3.2) is a Hamiltonian system. System (3.2) has a first integral (i.e. Hamiltonian function) given by

$$H(\phi, \varphi) = \frac{\varphi^2}{2} + V_i(\phi), \tag{3.4}$$

where $V_i(\phi) = -\int h_i(\phi) d\phi$.

The function $V_i(\phi)$ is called a potential energy function. This is due to its mechanical applications where it often corresponds to a stored energy [13], [63].

Any steady state of the system (3.2) must lie on the ϕ-axis and it corresponds to a critical point of the function $V_i(\phi)$. Hence, $V_i(\phi)$ determines the local behavior of the system (3.2). It can be shown [13], [128] that if the critical point of $V_i(\phi)$ is a local maximum (minimum) then the corresponding steady state of (3.2) is a saddle (center). Furthermore, if the leading term of $V_i(\phi)$ expanded about the critical point is cubic or higher then the steady state of (3.2) is degenerate.

Since $H(\phi, \varphi)$ is constant, it can provide us useful information on the global structure of the solution curves. Specifically, let $H(\phi, \varphi) = s$, then the solution curves are obtained from (3.4),

$$\varphi = \pm\sqrt{2(s - V_i(\phi))}. \tag{3.5}$$

An interesting property of these curves is the symmetry with respect to ϕ-axis. Then there are two major consequences of this symmetry.

1. If there are two saddle steady states with the same energy level (i.e. with the same maximum values of $V(\phi)$), with no higher energy level between them then they must be connected by heteroclinic orbits.

2. If there is a saddle and a center with no fluctuation in the energy level (i.e. with no critical point between the saddle and center), then the saddle is connected to itself with a homoclinic orbit.

The above mentioned points are of special interest since, in general, existence of a heteroclinic orbit is equivalent to existence of a traveling wavefront, while existence of a homoclinic orbit is equivalent to existence of a traveling wave pulse. Here, since the wave speed c is set to zero, the orbits correspond to stationary rather than traveling waves. Specifically, a stationary wavefront of (3.1) is a solution of (3.1) subject to boundary conditions $\lim \phi(t) = \phi_1$ as $t \to -\infty$ and $\lim \phi(t) = \phi_2$ as $t \to \infty$, where ϕ_1 and ϕ_2 are saddle-node or saddle-saddle steady states of (3.1), while a stationary wave pulse of (3.1) is subject to $\lim \phi(t) = \phi_j$ as $t \to \pm\infty$ where ϕ_j is a saddle steady state of (3.1).

In the following sections, existence of homoclinic and heteroclinic orbits will be discussed. In particular, the exact form of the homoclinic and heteroclinic orbits will be obtained according to the specific form of the birth function b_i for $i = 1, \ldots, 6$.

Concerning the local and global orbits of ODEs an underlying question is how to construct the phase-space of the ODEs. While numerical integrations and computer packages such as Matlab and Maple can help us to understand the behavior of the solution curves, they are limited to specific parameter values and the outcome may not represent all possible solution behaviors. Then one may naturally think of linearization about the steady states and use of the Hartman-Grobman Theorem [142] that guarantees topological conjugacy of the full nonlinear problem with the linearized system. Nevertheless, the effects of nonlinear terms are ignored and the phase-space of the linearized system may not reflect all features of the nonlinear problem. The rest of this section is devoted to construction of a phase-plane corresponding to the wave equation (3.1) and therefore to system (3.2). As mentioned above, the integral function $F(x)$ is constant along solution $x(t)$. The level sets of the function $F(x)$ are given by taking $F(x)$ =constant.

Definition 5. *A level set defined by $F(x) = k$, $k \in \mathbb{R}$ and fixed, consists of a family of orbits that is called an integral manifold.*

Clearly, the phase-plane of the system (3.2) consists of all integral manifolds of $H(\phi, \varphi)$. In the study of the local behavior of the level sets near the steady states, a useful tool is the Morse Lemma.

Definition 6. *Let $G : \mathbb{R}^n \to \mathbb{R}$ be C^∞ and the gradient $\frac{\partial G}{\partial x}(a) = 0$ with determinant $\left|\frac{\partial^2 G(a)}{\partial x^2}\right| \neq 0$. Then the point $x = a$ is called a non-degenerate critical point $G(x)$ and the function $G(x)$ is called a Morse-function in a neighborhood of $x = a$.*

The following lemma is due to American mathematician Marston Morse (1892-1977). It states that the behavior of a Morse-function G in a neighborhood of $x = a$ is determined by the quadratic part of the Taylor -expansion of G.

Lemma 7 (Morse)**.** Suppose that $x = 0$ is a non-degenerate critical point of the Morse-function $G(x)$ with expansion $G(x) = G_0 - c_1x_1^2 - \ldots - c_kx_k^2 + c_{k+1}x_{k+1}^2 + \ldots + c_nx_n^2$+higher order terms with positive coefficients $c_1, \ldots, c_n$; k is called the index of the critical point. Then in a neighborhood of $x = 0$, there exists a diffeomorphism $D : x \to y$ (i.e. a transformation which is one-to-one, unique C^1 and of which the inverse exists and is also C^1) that transforms $G(x)$ to $M(y)$ that is also a Morse-function and is given by

$$M(y) = M(0) - y_1^2 - \ldots - y_k^2 + y_{k+1}^2 + \ldots + y_n^2. \tag{3.6}$$

Concerning the wave equation (3.1) and the corresponding system (3.2), we find that the first integral $H(\phi, \varphi)$ is given by (3.4). Let $(\phi_j, 0)$ be a steady state of (3.2), then translating $(\phi_j, 0)$ to origin, $H(\phi, \varphi)$ in a neighborhood of the origin is a Morse-function with expansion

$$H(\phi, \varphi) = H(\phi_j, 0) + \frac{1}{2}\varphi^2 + \frac{1}{2}h_i'(\phi_j)(\phi - \phi_j)^2 + \text{higher order terms}, \tag{3.7}$$

where $h_i'(\phi_j) = d_m - \epsilon b'(\phi_j)$.

Using the Morse Lemma, if $h_i'(\phi_j) > 0$ then the index $k = 0$ and there exists a diffeomorphism to the quadratic form $y_1^2 + y_2^2$ which represents a center; if $h_i'(\phi_j) < 0$ then $k = 1$ and H is transformed to $y_1^2 - y_2^2$ which is a saddle. Therefore the linearization described in the previous chapter can be validated through Morse Lemma. Also, it can be seen that the Morse-function method coincides with the energy function method outlined above. What is added through the Morse-function method is the approximation of the orbits given by (3.7). Indeed, the method can also be applied to the non-conservative wave equation (i.e. when $c > 0$) to obtain approximation of orbits near the steady states ϕ_j of the general wave equation (2.8). The next section investigates periodic and nonperiodic behavior of wave solutions.

3.2 Periodic and nonperiodic stationary waves

The main purpose of this section is to demonstrate that under certain conditions the wave equation has no periodic solution. We also discuss the existence of periodic stationary wave solutions. In particular, for the case that $c = 0$ and $\alpha = 0$, we have the following proposition.

Proposition 6. Let $c = 0$, $\alpha = 0$ and ϕ_j be a steady state of (3.1), then the orbits of (3.2) near $(\phi_j, 0)$ are approximated by

$$H(\phi_j, 0) + \frac{1}{2}\varphi^2 + \frac{1}{2}\gamma(\phi - \phi_j)^2 = \frac{k}{2}, \tag{3.8}$$

where $k \in (-\infty, \infty)$ is any constant and $\gamma := d_m - \epsilon b'(\phi_j)$. Furthermore, if $\gamma > 0$ the orbits near $(\phi_j, 0)$ are closed and the periodic wave solutions are given by

$$\phi(t) = \frac{1}{\gamma}\sin(\sqrt{\gamma}t) + \phi_j. \tag{3.9}$$

Proof.

Using the Morse Lemma and the approximation (3.7), the phase-plane equation (3.8) is obtained. Considering that $\varphi = \frac{d\phi}{dt}$ and $\gamma > 0$, by letting $k = 2H(\phi_j, 0) + \frac{1}{\gamma}$ the wave solution (3.9) is obtained by integrating from the equation (3.8). □

Note that Proposition 6 is an improvement to some results for $c = 0$ obtained in previous chapter.

In order to study the reduced form of the wave equation, consider the following condition **A1**.

A1) $c = 0$ and $\alpha = 0$.

Furthermore, let the birth function $b(\phi)$ satisfy the following two conditions.

A2) $b(0) = 0$, $\epsilon b(\phi) > d_m\phi$ for $\phi < 0$ and $\epsilon b(\phi) < d_m\phi$ for $\phi > 0$.

A3) $\int_0^z (\epsilon b(s) - d_m s)ds \to -\infty$ if $z \to \pm\infty$.

The following Proposition says that under conditions **A1**, **A2** and **A3** the population model admits no periodic stationary wave.

Proposition 7. If conditions **A1**, **A2** and **A3** are satisfied, then equation (3.2) has no periodic solution.

Proof.

Condition **A1** reduces the general wave equation to (3.2). Condition **A2** implies that origin is the only steady state of (3.2). It also implies that origin is a local maximum of the potential function $V(\phi)$ of (3.2). Furthermore, condition **A3** guarantees that origin is the only extermum of the potential function. Hence, the only steady state of (3.2) is a saddle at origin. The proof is complete. □

Remark 17. An example of nonexistence of periodic solutions is when the birth function b_1 is considered. If $\frac{\epsilon p}{d_m} < 1$, $c = 0$ and $\alpha = 0$, then all conditions of the proposition are satisfied and the wave solution does not have any periodic behavior.

Remark 18. If condition **A2** is modified in a way that $\epsilon b(\phi) < d_m \phi$ for $\phi < 0$ and $\epsilon b(\phi) > d_m \phi$ for $\phi > 0$ and in condition **A3**, the integral tends to $+\infty$ then using a similar argument it can be shown that origin is the only steady state and it is a center. Hence all wave solutions are periodic. Nevertheless, this is biologically unrealistic since solution ϕ can become negative.

Conditions **A2** and **A3** are too restrictive, then we may think of other methods to prove existence or nonexistence of periodic solutions. Since the wave equation is of second order, several theorems of planar systems are applicable to it. While Lienard's Theorem [142] can be used to establish existence of limit cycles for certain planar systems, there are criteria such as Bendixon's or Dulac's criteria that can be used to investigate nonexistence of closed orbits (i.e. limit cycles). The following theorem is due to French mathematician Henry Dulac (1870-1955).

Theorem 11. (Dulac's Criteria) For the system $\dot{x} = X(x, y)$, $\dot{y} = Y(x, y)$ there are no closed paths in a simply connected region in $\mathbb{R}^2$ in which $\frac{\partial(\rho X)}{\partial x} + \frac{\partial(\rho Y)}{\partial y}$ is of one sign, where $\rho(x, y)$ is any function having continuous first partial derivatives.

Proof.

The proof is given on page 247 of [107] which is an application Green's Theorem (see also Problem 2 in Section (3.9) of [142]). □

Let $\alpha = 0$ and $\varphi = \frac{d\phi}{dt}$, then the wave equation (3.1) is written as a system of first order equations,

$$\begin{cases} \frac{d\phi}{dt} &= \varphi \\ \frac{d\varphi}{dt} &= \frac{1}{D_m}(c\varphi + d_m\phi - \epsilon b(\phi(t - c\tau)) \end{cases} \tag{3.10}$$

Let $\rho(\phi, \varphi)$ be a real valued function with continuous first order partial derivatives. Define the function $G : \mathbb{R}^2 \to \mathbb{R}^2$,

$$G(\phi, \varphi) := \frac{\partial}{\partial \phi}(\rho \frac{d\phi}{dt}) + \frac{\partial}{\partial \varphi}(\rho \frac{d\varphi}{dt}). \tag{3.11}$$

Denote ρ_ϕ and ρ_φ as partial derivatives of ρ with respect to ϕ and φ, then using the righthand sides of (3.10), $G(\phi,\varphi)$ is written,

$$\begin{aligned} G(\phi,\varphi) = \; & \rho_\phi\varphi + \rho\tfrac{d\varphi}{d\phi} + \tfrac{1}{D_m}\rho_\varphi(c\varphi + d_m\phi + \epsilon b(\phi)(t-c\tau)) \\ & + \tfrac{1}{D_m}\rho(c + d_m\tfrac{d\phi}{d\varphi} - \tfrac{\epsilon d b(\phi(t-c\tau))}{d\varphi}). \end{aligned} \tag{3.12}$$

Let $X = \frac{d\varphi}{d\phi}$ and apply the chain rule for the last term in (3.12), we get that,

$$G(\phi,\varphi) = \rho_\phi\varphi + X(\rho + \rho_\varphi\varphi) + \frac{\rho}{D_m X}(d_m - \epsilon b'(\phi(t-c\tau))) + \frac{c}{D_m}\rho. \tag{3.13}$$

We use the expression (3.13) to prove that under certain conditions the stationary wave solution of the population model is nonperiodic.

Proposition 8. Let $\alpha = 0$ and $c = 0$. Let $d_m - \epsilon b'(\phi) > 0$ for all $\phi \in \Omega \subseteq \mathbb{R}$, then the system (3.10) has no closed orbit in $\Omega \times \mathbb{R}$ and therefore the wave equation (3.1) has no periodic solution.

Proof.

Let $\rho(\phi,\varphi) = \varphi(d_m\phi - \epsilon b(\phi))$ using the righthand side of (3.10) we can see that $X = \frac{(d_m\phi - \epsilon b(\phi))}{D_m\varphi} = \frac{\rho}{D_m\varphi^2}$. Hence expression (3.13) takes the form

$$G(\phi,\varphi) = 2\varphi^2(d_m - \epsilon b'(\phi)) + 2\rho X + \varphi^2(d_m - \epsilon b'(\phi)) > 0. \tag{3.14}$$

Using Dulac's criteria, the proof is complete. □

Here for the case that $c = 0$, $\alpha = 0$, $b(\phi) = b_i(\phi)$, $i = 1,2,3$ and $d_m - \epsilon p > 0$, the wave equation (3.1) admits no periodic solution. Note that the condition $d_m - \epsilon p > 0$ implies $d_m - \epsilon b_i'(\phi) > 0$ for $i = 1,2,3$. Another way of getting the same conclusion is the Poincare-Bendixon's Theorem. When $d_m - \epsilon p > 0$, the origin is the only steady state of the system (3.10). Since $b_i(0) = p$ for $i = 1,2,3$, by Lemma 4, the origin is a saddle. Hence the (ϕ,φ) phase-plane has no closed orbits. One can simply derive a contradiction by considering a closed orbit and using the Poincare-Bendixon

Theorem.

Similarly, for $c = 0$, $\alpha = 0$, $b(\phi) = b_i(\phi)$, $i = 4, 5, 6$ and $\frac{\epsilon p}{d_m} < ae$, the wave equation has no periodic solution. The above conclusions are true only when the real domain is considered. In the complex domain, the wave equation has a positive steady state when $b(\phi) = b_i(\phi)$, $i = 1, 2, 3$, $d_m - \epsilon p > 0$ and $q^{-1} = 2k$, $k \in \mathbb{Z}\backslash\{0\}$. It can be shown that under some conditions, periodic and homoclinic wave solutions exist even though $d_m - \epsilon b_i^{'}(\phi) > 0$. The study of existence and nonexistence of periodic wave solutions will continue in Chapter 4.

Using the energy function method it can be seen that a minimum (maximum) of $V_i(\phi)$ corresponds to a center (saddle) steady state of the wave equation (3.17). In the following two sections, existence of homoclinic and heteroclinic stationary waves is demonstrated. Specifically, with any of the birth functions $b(\phi) = b_i(\phi)$ $i = 1, \ldots, 6$ the wave equation admits a homoclinic stationary wave solution while the birth function b_4 gives rise to existence of a heteroclinic stationary wave solution. In addition, existence of periodic stationary wave solutions has been numerically investigated.

3.3 Stationary wave pulses

As mentioned in the previous chapter, when $\alpha = 0$, the original RD equation (2.7) and therefore the corresponding wave equation (2.8) are respectively reduced to the forms,

$$\frac{\partial w}{\partial t} = D_m \frac{\partial^2 w}{\partial x^2} - d_m w + \epsilon b(w(t - \tau, x)), \tag{3.15}$$

$$\phi'' - \frac{c}{D_m}\phi' - \frac{d_m}{D_m}\phi + \frac{\epsilon}{D_m} b(\phi(t - c\tau)) = 0. \tag{3.16}$$

Recall the specific birth functions b_i, $i = 1, \ldots, 6$ that are in the following forms.

$$b_1(\phi) = p\phi e^{-a\phi^q},$$

$$b_2(\phi) = \frac{p\phi}{1 + a\phi^q},$$

$$b_3(\phi) = \begin{cases} p\phi(1 - \frac{\phi^q}{k_c^q}) & 0 \leq \phi \leq k_c \\ 0 & \phi > k_c, \end{cases}$$

$$b_4(\phi) = p\phi^2 e^{-a\phi},$$

$$b_5(\phi) = \frac{p\phi^2}{1 + a\phi},$$

$$b_6(\phi) = \frac{p\phi^2}{(1 + a\phi)^2}.$$

where p, q, a and k_c are all positive constants.

When $c = 0$ and $\alpha = 0$ the wave equation (3.16) is reduced to

$$\phi'' - \frac{d_m}{D_m}\phi + \frac{\epsilon}{D_m} b_i(\phi) = 0. \tag{3.17}$$

equation (3.17) is a conservative system of the form

$$\phi'' = g_i(\phi), \tag{3.18}$$

where

$$g_i(\phi) = \frac{1}{D_m}(d_m\phi - \epsilon b_i(\phi)).$$

Specifically the conservative system corresponding to (3.17) is given by

$$\begin{cases} \phi' &= \varphi, \\ \varphi' &= g_i(\phi). \end{cases} \tag{3.19}$$

Define the potential function as

$$V_i(\phi) = -\int g_i(\phi) d\phi. \tag{3.20}$$

Then using the system (3.19) we have

$$\int \varphi d\varphi = \int g_i(\phi)d\phi, \tag{3.21}$$

and therefore

$$\varphi = \pm\sqrt{2}(s_i - V_i(\phi))^{\frac{1}{2}}, \tag{3.22}$$

where s_i is a constant that will be determined according to each $V_i(\phi)$.

As mentioned before, a stationary wavefront of (3.15) is a solution of (3.17) that satisfies the boundary conditions $\lim \phi(t) = \phi_1$ as $t \to -\infty$ and $\lim \phi(t) = \phi_2$ as $t \to \infty$, where ϕ_1 and ϕ_2 are steady states of (3.17). The reduced model (3.15) has a stationary wave pulse if it satisfies (3.17) and the boundary conditions with $\phi_1 = \phi_2$.

We have the following proposition for the case that the birth function b_1 is considered.

Proposition 9. If $b(\phi) = b_1(\phi), c = 0,\ \alpha = 0,\ q^{-1} = 2k,\ k \in \mathbb{Z}\backslash\{0\}$ and $\frac{\epsilon p}{d_m} < 1$, then system (3.19) has a homoclinic orbit and the model (3.15) admits a stationary wave pulse.

Proof.

The corresponding wave equation and phase path are respectively given by

$$\phi'' - \frac{d_m}{D_m}\phi + \frac{\epsilon p}{D_m}\phi e^{-a\phi^q} = 0, \tag{3.23}$$

$$\varphi = \pm\sqrt{2}(s_1 - V_1(\phi))^{\frac{1}{2}}, \tag{3.24}$$

where s_1 is a constant and V_1 is calculated as follows,

$$V_1(\phi) = \frac{1}{D_m}\left(-\frac{d_m}{2}\phi^2 + \epsilon p \int \phi e^{-a\phi^q} d\phi\right).$$

Let $\psi = a\phi^q$, then the last integral is written as

$$I_1 = \frac{\epsilon p}{q a^{2/q}} \int \psi^{\frac{2}{q}-1} e^{-\psi} d\psi. \tag{3.25}$$

Let $q^{-1} = 2k$ with $k \in \mathbb{Z}^+\backslash\{0\}$, then using integration by parts we have

$$I_1 = \frac{2k\epsilon p}{a^{4k}} \int \psi^{4k-1} e^{-\psi} d\psi = \frac{2k\epsilon p}{a^{4k}} \left(-\psi^{4k-1} e^{-\psi} + (4k-1) \int \psi^{4k-2} e^{-\psi} d\psi \right).$$

Using induction over k we get that

$$I_1 = -\frac{2k\epsilon p}{a^{4k}} \left(\sum_{m=0}^{4k-1} \frac{(4k-1)!}{m!} \psi^m \right) e^{-\psi} = -\frac{2k\epsilon p}{a^{4k}} \left(\sum_{m=0}^{4k-1} a^m \frac{(4k-1)!}{m!} \sqrt[2k]{\phi^m} \right) e^{-a \sqrt[2k]{\phi}}.$$

Hence the phase path is given by

$$\varphi(\phi) = \pm\sqrt{2} \left(s_1 + \frac{d_m}{2D_m} \phi^2 - I_1 \right)^{\frac{1}{2}}.$$

Let $s_1 = -\frac{2k\epsilon p}{a^{4k}}(4k-1)!$, then $\varphi(\phi_1) = 0$ and we have

$$\varphi(\phi) = \pm\sqrt{2} \left(\frac{+d_m}{2D_m} \phi^2 + \frac{2k\epsilon p}{a^{4k}} \left(\sum_{m=1}^{4k-1} \frac{a^m (4k-1)!}{m!} \sqrt[2k]{\phi^m} \right) e^{-a \sqrt[2k]{\phi}} \right)^{\frac{1}{2}}. \tag{3.26}$$

Similar to Lemma 4 we have that $\phi_1 = 0$ and $\phi_2 = (\frac{1}{a} \ln \frac{\epsilon p}{d_m})^{\frac{1}{q}}$ are respectively saddle and center steady states. Hence $V_1(\phi_1)$ is a maximum value while $V_1(\phi_2)$ is a minimum value. Moreover, ϕ_1 and ϕ_2 are the only steady states of (3.17). Then considering the general form (3.24) we get that $|\varphi(\phi)|$ has only two extrema: a minimum at $(\phi, |\varphi(\phi_1)|) = (0,0)$ and a maximum at $(\phi_2, |\varphi(\phi_2)|)$. Note that $\sqrt[2k]{\phi}$ is in fact a root of the equation $z^{2k} = \phi$ with $\phi > 0$. This equation in the complex domain has always the root $z = \sqrt[2k]{\phi} e^{i\pi}$. Since there is no other extrema greater than ϕ_2 by considering the root $\sqrt[2k]{\phi} e^{i\pi}$, the last term in (3.26) becomes negative and dominant as ϕ increases. Then there exists $\phi_r > \phi_2$ such that $|\varphi(\phi_r)| = 0$. Noting that $\varphi(\phi)$ in (3.26) is symmetric with respect to ϕ axis we have a closed orbit $\Gamma(\phi), \phi \in [0, \phi_1]$ (i.e. $\Gamma(\phi)$ is a homoclinic path) around ϕ_2 which joins ϕ_1 to itself. $\square$

Remark 19. In the real domain when $b(\phi) = b_1(\phi)$, it is possible to obtain a homoclinic path for the case that $\frac{\epsilon p}{d_m} > 1$. But in that case, as shown in Lemma 4 the steady state ϕ_1 is a center while the ϕ_2 is a saddle. This results in a homoclinic path with negative ϕ values that make the problem physically unrealistic.

Remark 20. In general, when the birth function $b_1(\phi), b_2(\phi)$ or $b_3(\phi)$ is considered, using the root $\phi^q = \sqrt[2k]{\phi}e^{i\pi}$ is equivalent to modifying these birth functions to the following forms. $b_1(\phi) = p\phi e^{a\phi^q}$, $b_2(\phi) = \frac{p\phi}{1-a\phi^q}$,

$$b_3(\phi) = \begin{cases} p\phi(1 + \frac{\phi^q}{k_c^q}) & 0 \leq \phi \leq k_c \\ 0 & \phi > k_c, \end{cases}$$

where p, q, a and k_c are positive constants.

Remark 21. The steady state $\phi_2 > 0$ exists only when in the equation $\epsilon e^{-a\phi^q} = d_m$, $\phi^q = \sqrt[2k]{\phi}e^{i\pi}$. This may seem as a limitation, but it will be removed when other birth function such as b_4, b_5 are employed.

Remark 22. Existence of a homoclinic or heteroclinic paths is equivalent to existence of wave solution. By letting $\varphi = \frac{d\phi}{dt}$ in equation (3.26), the wave solution ϕ can be obtained. Nevertheless solving such an equation seems as difficult as solving the original wave equation (3.17).

Remark 23. By letting $r = \frac{2}{q} - 1$, the integral term in (3.25) has the following general solution,

$$\int \psi^r e^{-\psi} d\psi = \psi^{(\frac{r}{2})} e^{(\frac{-\psi}{2})} \frac{W_h(\frac{r}{2}, \frac{r}{2} + \frac{1}{2}, \psi)}{1+r}, \tag{3.27}$$

where W_h is the Whitaker Function M (see [159] for more details) which is a standard form of confluent hypergeometric function. Basically, it is the solution of the Whitaker equation

$$u''(z) + \left(\frac{-1}{4} + \frac{k}{z} + \frac{\frac{1}{4} - \mu^2}{z^2}\right) u(z) = 0, \tag{3.28}$$

where $k = \frac{r}{2}$ and $\mu = \frac{r}{2} + \frac{1}{2}$.

The solution (3.27) suggests a connection between the equation (3.23) and the Whitaker equation (3.28).

Existence of homoclinic path for the case that $\tau c > 0$ is discussed in the next section. The following Proposition establishes the existence of a homoclinic path for (3.16) when the birth function b_2 or b_3 are considered.

Proposition 10. The wave equation (3.17) with birth function b_2 or b_3 admits a homoclinic path between its saddle ϕ_1 and center ϕ_2 when $c = 0$, $\alpha = 0$, $q^{-1} = 2k$, $k \in \mathbb{Z}\backslash\{0\}$ and $\frac{\epsilon p}{d_m} < 1$ with the additional condition $\frac{1}{2} < \frac{\epsilon p}{d_m}$ when b_3 is considered.

Proof.

Condition $\frac{1}{2} < \frac{\epsilon p}{d_m}$ for b_3 is required for existence of $\phi_2 > 0$ in the complex domain. Similar to Lemma 4 it can be shown that when $\frac{\epsilon p}{d_m} < 1$ and $q^{-1} = 2k$, ϕ_1 and ϕ_2 are saddle and center of (3.17) respectively. Consider b_2 as the birth function. Then we have

$$\phi'' - \frac{d_m}{D_m}\phi + \frac{\epsilon p}{D_m}\frac{\phi}{1 + a\phi^q} = 0, \tag{3.29}$$

$$\varphi(\phi) = \pm\sqrt{2}(s_2 - V_2(\phi))^{\frac{1}{2}}, \tag{3.30}$$

where

$$V_2(\phi) = \frac{1}{D_m}\left(-\frac{d_m}{2}\phi^2 + \epsilon p\int \frac{\phi}{1 + a\phi^q}d\phi\right). \tag{3.31}$$

Let $\psi = 1 + a\phi^q$ then the last integral is written as

$$I_2 = \frac{\epsilon p}{qa^{\frac{2}{q}}}\int (\psi - 1)^{\frac{2}{q}-1}\psi^{-1}d\psi. \tag{3.32}$$

Since $q^{-1} = 2k$ with $k \in \mathbb{Z}^+ \setminus \{0\}$, using integration by parts we get that

$$I_2 = \frac{\epsilon p}{qa^{\frac{2}{q}}}\left(\sum_{n=0}^{4k-2}\binom{4k-1}{n}\frac{(-1)^n\psi^{4k-(1+n)}}{4k - (1+n)} + \ln\psi\right). \tag{3.33}$$

In order to have a path $(\phi, \varphi(\phi))$ passing through the origin we should have $s_2 = V_2(0)$, then the phase path is given by

$$\varphi = \pm\sqrt{2}\left(V_2(0) + \frac{1}{D_m}\left(\frac{d_m}{2}\phi^2 - I_2(\phi)\right)\right). \tag{3.34}$$

But ϕ_1 and ϕ_2 are the only steady states of (3.17). Hence ϕ_1 and ϕ_2 are the only extrema of $|\varphi|$. Since ϕ_1 and ϕ_2 are respectively saddle and center, they are respectively the minimum and maximum $|\varphi|$. Since the dominant term in (3.33) is $-(1+a\phi^q)^{4k-1} < 0$ for $\phi > 0$, we get that $\varphi(\phi_r) = 0$ for some $\phi_r > \phi_2$. Since $\varphi(\phi)$ is symmetric with respect to ϕ axis there exists the homoclinic path $\Gamma(\phi)$, $\phi \in [0, \phi_r]$. Consider now b_3 as the birth function. Then similar to the above procedure,

$$\varphi = \pm\sqrt{2}(s_3 - V_3(\phi))^{\frac{1}{2}}, \tag{3.35}$$

$$V_3(\phi) = \frac{1}{D_m}\left(-\frac{d_m}{2}\phi^2 + \epsilon p \int \phi(1 - \frac{\phi^q}{k_c^q})\right), \tag{3.36}$$

$$= \frac{1}{D_m}\phi^2\left(\frac{-d_m + \epsilon p}{2} - \frac{\epsilon p}{(q+2)k_c^q}\phi^q\right). \tag{3.37}$$

Let $s_3 = 0$. Again ϕ_1 and ϕ_2 are the only steady states and they are saddle and center respectively. Hence there is a path Γ connecting $(\phi_1, 0)$ to itself. $\square$

Remark 24. Under conditions of the Proposition 10 the model (3.15) with birth function $b_2(\phi)$ or $b_3(\phi)$ admit a stationary wave pulse.

Remark 25. The integral term in (3.31) has the following general solutions

$$\int \frac{\phi}{1 + a\phi^q} d\phi = \frac{1}{2}\phi^2 \text{ hypergeom } \left(\left[1, \frac{2}{q}\right], \left[1 + \frac{2}{q}\right], -a\phi^q\right),$$

where hypergeom is the generalized hypergeometric function arising from the hypergeometric differential equation

$$z(1-z)\frac{d^2\phi}{dz^2} + (c - (a+b+1)z)\frac{d\phi}{dz} - ab\phi = 0.$$

Using the rising factorial or Pochhammer symbol:

$$(a)n = a(a+1)(a+2)\dots(a+n-1), (a)_0 = 1.$$

The function generalized hypergeometric can be represented as the convergent series,

$$\text{hypergeom}\left([a_1, \dots, a_p], [b_1, \dots, b_q]; z\right) = \sum_{n=0}^{\infty} \frac{(a_1)_n \dots (a_p)_n}{(b_1)_n \dots (b_q)_n} \frac{z^n}{n!}.$$

Several elementary functions (e.g. $\arcsin(z)$, $\arctan(z)$ and $(1-z)^k$), Bessel functions, error function (i.e. $\frac{2}{\sqrt{\pi}} \int_0^x e^{-t^2} dt$) and elliptic integrals are all special forms of the hypergeometric function (see Chapter 15 of [1]).

When $q^{-1} = 2k$ we have

$$\int \frac{\phi}{1 + a\phi^q} = \int \frac{\phi}{1 + a\sqrt[2k]{\phi}} = 2k\phi L_\Phi(-a\sqrt[2k]{\phi}, 1, 4k),$$

where L_Φ is the Lerch phi (Lerch transcendent) function [78] with the following general form,

$$L_\Phi(z, s, v) = \sum_{n=0}^{\infty} \frac{z^n}{(n+v)^s}.$$

Existence of periodic stationary wave solutions and stationary wave pulses are numerically verified. Similar to the previous chapter the toolbox “pplane7 ” is employed to generate the phase-planes (See http://math.rice.edu/∼ dfield for more details). Also the stationary and periodic wave solutions are numerically obtained with Matlab ODE solver “ode45”. Figure 3.1 represents phase-plane, periodic waves and wave pulses with respect to the birth functions $b_1(\phi)$ and $b_2(\phi)$. Namely, for the first column of plots the birth function $b(\phi) = b_1(\phi)$ has been used and the parameter values are $\epsilon = 1, d_m = 1, D_m = 1, p = 0.4, a = 1, q = 0.5$. The second column represents the same qualities from top to bottom. Instead the birth function $b(\phi) = b_2(\phi)$ has been used and the parameter values are $\epsilon = 1, d_m = 1, D_m = 1, p = 0.3, a = 0.2, q = 0.5,$. Also Figures 3.2 and 3.3 represent phase-plane, periodic stationary wave solutions and stationary wave pluses when the birth functions $b_i(\phi), i = 3, \dots, 6$ are used. Details of the Figure 3.2 and the parameter values are given below. First column: $b(\phi) = b_3(\phi), \epsilon = 2, d_m = 3, D_m = 1, p = 1, k = 4, q = 0.5$, Second column: $b(\phi) = b_4(\phi), \epsilon = 1, d_m = 1, D_m = 1, p = 7, a = 2.$

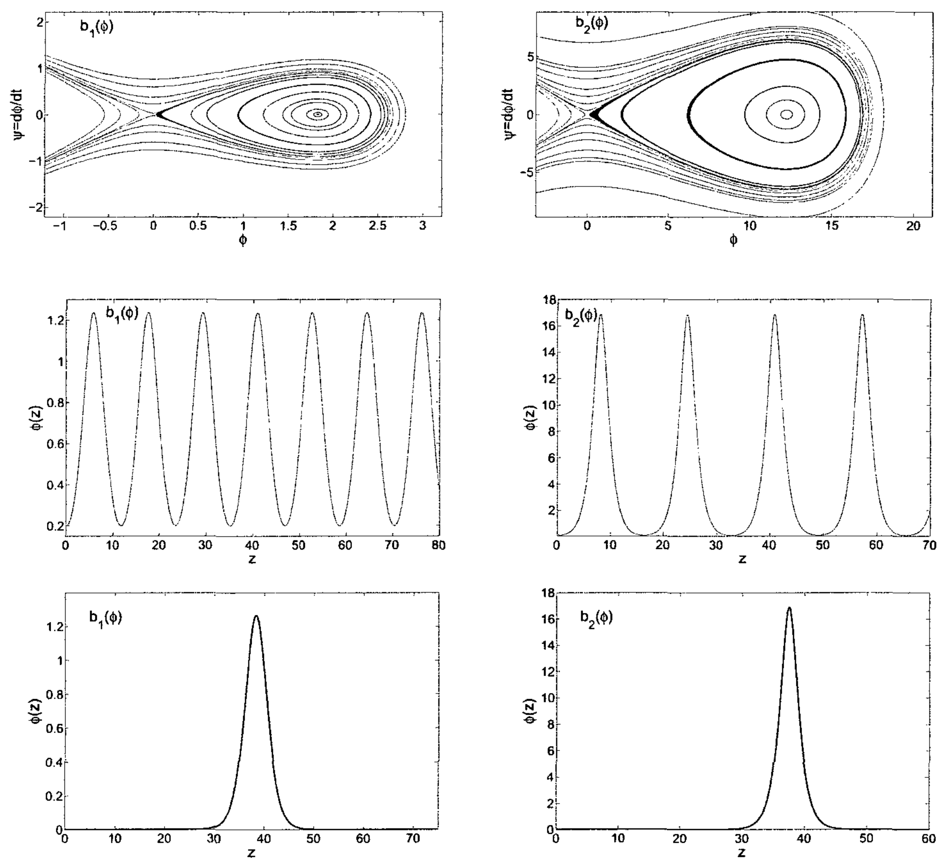


Figure 3.1: From top to bottom, each column of the Figures represent respectively the phase-plane, a stationary periodic wave and the stationary wave pulse when $\alpha = 0$ and $c = 0$.

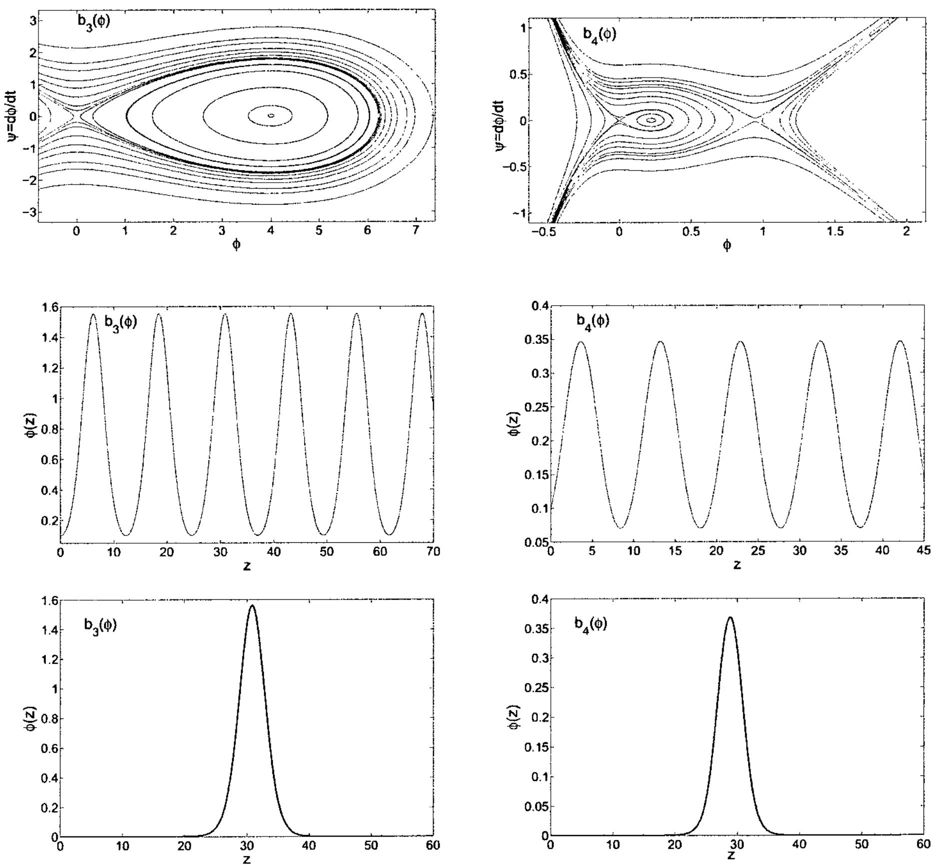


Figure 3.2: Similar to the Figure 3.1, from top to bottom the first and the second column represent respectively the phase-plane, a stationary periodic wave and the stationary wave pulse when $\alpha = 0$ and $c = 0$.

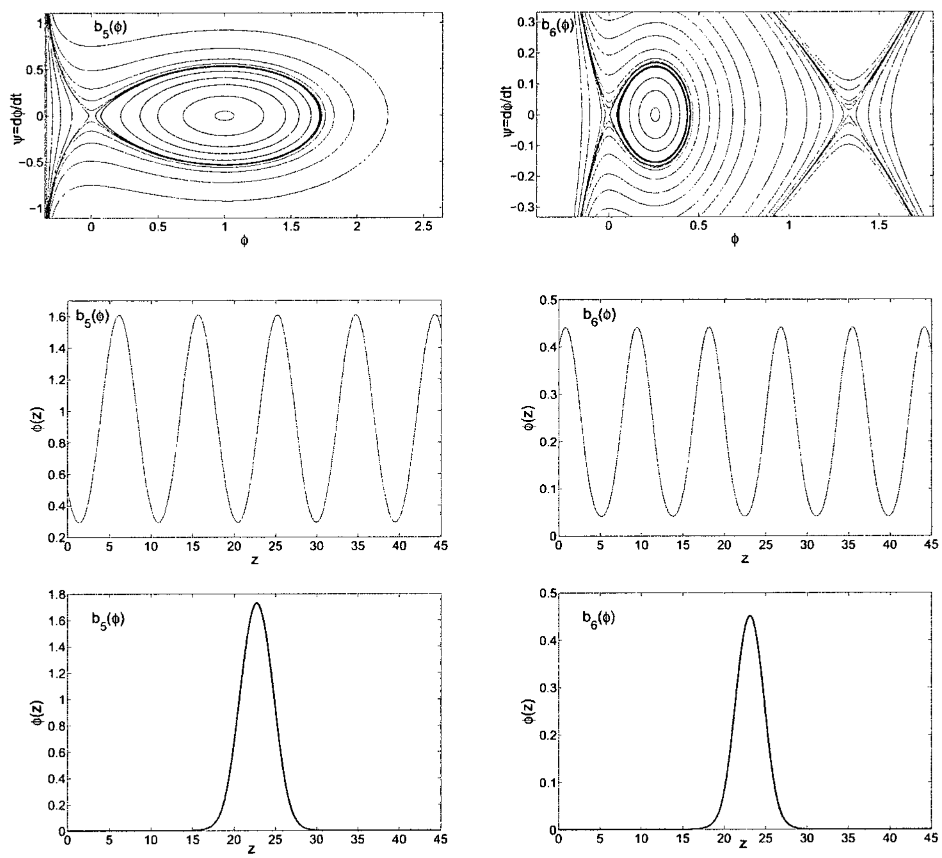


Figure 3.3: From top to bottom the first and the second column represent respectively the phase-plane, a stationary periodic wave and the stationary wave pulse when $\alpha = 0$ and $c = 0$.

Also details of the Figure 3.3 and the parameter values are given below. First column: $b(\phi) = b_5(\phi), \epsilon = 1, d_m = 2, D_m = 1, p = 8, a = 3$; Second column: $b(\phi) = b_6(\phi), \epsilon = 2, d_m = 2, D_m = 1, p = 8, a = 1.7$.

Note that $b_4(\phi)$ has been considered in the real domain. We will use $b_4(\phi)$ to prove existence of heteroclinic orbits. All other cases described above are valid only when $\phi^q = \sqrt[2k]{\phi}e^{i\pi}$. In fact, when $b_1(\phi), b_2(\phi)$ or $b_3(\phi)$ is considered in the real domain, the only steady state is $\phi_1 = 0$. Since a large portion of research in mathematical biology is carried out in real domain, it is more compelling to study stationary wave pulses in the real domain. In our case, when the birth function b_5 is considered the wave equation admits two steady states that are obtained in the real domain. Similar to Propositions 9 and 10, in the following it will be shown that the wave equation (3.17) admits a homoclinic orbit when b_5 is considered.

Proposition 11. Let $\frac{\epsilon p}{d_m} > a$, $c = 0$ and $\alpha = 0$. Then the wave equation (3.17) with the birth function b_5 has a homoclinic orbit in the real domain.

Proof.

The steady state ϕ_2 exists under the condition $\frac{\epsilon p}{d_m} > a$. Similar to the previous proof,

$$\varphi(\phi) = \pm\sqrt{2}(s_5 - V_5(\phi))^{\frac{1}{2}}, \tag{3.38}$$

where s_5 is a constant and V_5 is obtained as follows,

$$\begin{aligned} V_5(\phi) &= \frac{1}{D_m}(-d_m \int \phi d\phi + \epsilon p \int \frac{\phi^2}{1+a\phi} d\phi) \\ &= \frac{1}{D_m}(\frac{-d_m}{2}\phi^2 + \frac{\epsilon p}{2a^3}((1+a\phi)^2 - 4(1+a\phi) + 2\ln|1+a\phi|)). \end{aligned} \tag{3.39}$$

Let $s_5 = \frac{-3\epsilon p}{2D_m a^3}$, then $(\phi_1, \varphi(\phi_1)) = (0, 0)$. Since ϕ_1 and ϕ_2 are the only extrema of $\varphi(\phi)$, the leading order is $(\frac{\epsilon p}{2a} - \frac{d_m}{2})\phi^2 < 0$ and $\varphi(\phi)$ is symmetric with respect to the ϕ axis, the same argument is applied here and there exists a homoclinic orbit connecting ϕ_1 to itself. $\square$

The next section deals with stationary wavefronts of the population model.

3.4 Stationary wavefronts

The main difference between the birth functions b_4, b_6 and the other ones is that b_4 and b_6 admit an inflection point in their graphs. Hence the line $d_m w$ can intersect the curve $\epsilon b_i(w)$ at three points giving rise to three distinct steady states. As shown in Lemma 4, two of these (i.e. ϕ_1 and ϕ_3) are saddles while the one in the middle (i.e. ϕ_2) is a center steady state. Then it is reasonable to expect a heteroclinic path connecting ϕ_1 to ϕ_3 under certain circumstances. The following Proposition demonstrates existence of a heteroclinic path when $b_4(\phi)$ is considered; also the nonexistence of heteroclinic path is shown when $b_6(\phi)$ is considered.

Proposition 12. Let $c = 0$ and $\alpha = 0$. If $\frac{\epsilon p}{d_m} \approx 2.94a$ then the wave equation (3.17) with birth function b_4 has a heteroclinic path. Moreover, the wave equation (3.17) does not admit any heteroclinic path when b_6 is considered.

Proof.

When b_4 is considered we have,

$$\varphi(\phi) = \pm\sqrt{2}(s_4 - V_4(\phi))^{\frac{1}{2}},$$

where $V_4(\phi)$ is calculated as follows,

$$\begin{aligned} V_4(\phi) &= \tfrac{1}{D_m}(-d_m \textstyle\int \phi d\phi + \epsilon p \int \phi^2 e^{-a\phi}), \\ &= \tfrac{-1}{D_m}(\tfrac{d_m}{2}\phi^2 + \tfrac{\epsilon p}{a}(\phi^2 + \tfrac{2}{a}\phi + \tfrac{2}{a^2})e^{-a\phi}). \end{aligned} \tag{3.40}$$

Let $s_4 = -\frac{2\epsilon p}{a^3 D_m}$ then $(\phi_1, \varphi(\phi_1)) = (0,0)$. By Lemma 4 ϕ_1 and ϕ_3 are saddles, while ϕ_2 is a center. Hence $|\varphi(\phi)|$ has minimum value at ϕ_1 and ϕ_3 and has a maximum values at ϕ_2. We need to show that $\varphi(\phi_3) = 0$. Let

$$\frac{\epsilon p}{d_m} = \frac{ae^k}{k}, \tag{3.41}$$

for $k > 1$; then

$$\phi_3 = \frac{k}{a}. \tag{3.42}$$

Substituting (3.41) and (3.42) into $\frac{1}{2}(\varphi(\phi_3))^2$ we get that,

$$\begin{aligned} s_4 - V_4(\phi_3) &= \tfrac{d_m}{D_m}\left(-\tfrac{2\epsilon p}{a^3 d_m} + \tfrac{k^2}{2a^2} + \tfrac{\epsilon p}{a d_m}(\tfrac{k^2+2k+2}{a^2})e^{-k}\right), \\ &= \tfrac{d_m}{D_m a^2}\left(-\tfrac{2e^k}{k} + \tfrac{k^2}{2} + k + 2 + \tfrac{2}{k}\right), \end{aligned} \tag{3.43}$$

which has a root $k_r > 1$. This is due to the fact that for $k = 1$, equation (3.43) is positive and it becomes negative as k increases. In fact $k_r \approx 1.45$. Thus, for $\phi_3 = \frac{k_r}{a}$ we have $s_4 - V_4(\phi_3) = 0$ which gives rise to $\varphi(\phi_3) = 0$.

When b_6 is considered we have,

$$\varphi(\phi) = \pm\sqrt{2}(s_6 - V_6(\phi))^{\frac{1}{2}},$$

where $V_6(\phi)$ is obtained as follows,

$$\begin{aligned} V_6(\phi) &= \tfrac{1}{D_m}\left(-d_m \int \phi d\phi + \epsilon p \int \tfrac{\phi^2 d\phi}{(1+a\phi)^2}\right), \\ &= \tfrac{1}{D_m}\left(-d_m\phi^2 + \tfrac{\epsilon p}{a^3}(1 + a\phi - \tfrac{1}{1+a\phi} - 2\ln|1 + a\phi|)\right). \end{aligned} \tag{3.44}$$

Let $s_6 = 0$, then $(\phi_1, \varphi(\phi_1)) = (0, 0)$. Then we are required to have $\varphi(\phi_3) = 0$. Noting that $\phi_3 > \frac{1}{a}$, there exists $k > 1$ such that $\phi_3 = \frac{k}{a}$. Then we have $\frac{\epsilon p}{d_m} = \frac{a(1+k)^2}{k}$. Similar to the procedure above we get that,

$$\begin{aligned} s_6 - V_6(\phi_3) &= -\tfrac{d_m}{D_m}\left(-\tfrac{k^2}{a^2} + \tfrac{\epsilon p}{d_m a^3}(1 + k - \tfrac{1}{1+k} - 2\ln(1 + k))\right) \\ &= \tfrac{-d_m}{k D_m a^2}\left(3k^2 + 2k - 2(1 + k)^2 \ln(1 + k)\right) > 0, \end{aligned} \tag{3.45}$$

for all $k > 1$.

Hence, there is no path connecting ϕ_1 to ϕ_3. $\square$

Remark 26. The coefficient 2.94 in Proposition 12 is obtained from $\frac{e^{k_r}}{k_r}$, where k_r is the root of $-\frac{2e^k}{k} + \frac{k^2}{2} + k + 2 + \frac{2}{k}$.

Our numerical simulations confirm the existence of stationary wavefronts of the model (3.15). Figure 3.4 represents such a quality . Also the phase-plane and periodic stationary waves have been plotted. Details of the Figures and the parameter values are given below. $b(\phi) = b_4(\phi), \epsilon = 1, d_m = 1.7, D_m = 1, p = 9.99, a = 2$.

In summary, this chapter is concerned with the stationary wave pulses and wavefronts of the model. The method of energy function can be used to find the explicit phase-plane wave solutions of the model. Presence of the stationary wave solutions of the model is an interesting factor that can explain some underling ecological mechanisms. For instance, formation of a stationary pulse in the spatial domain may correspond to a permanent (or long term) migration of a population scattered in the spatial domain. This becomes more meaningful in dynamical studies of the certain species that invade the breeding area for more than a year (see for example chapter 6 of [195]).
In the next chapter we provide a detailed analysis of traveling wave solutions.

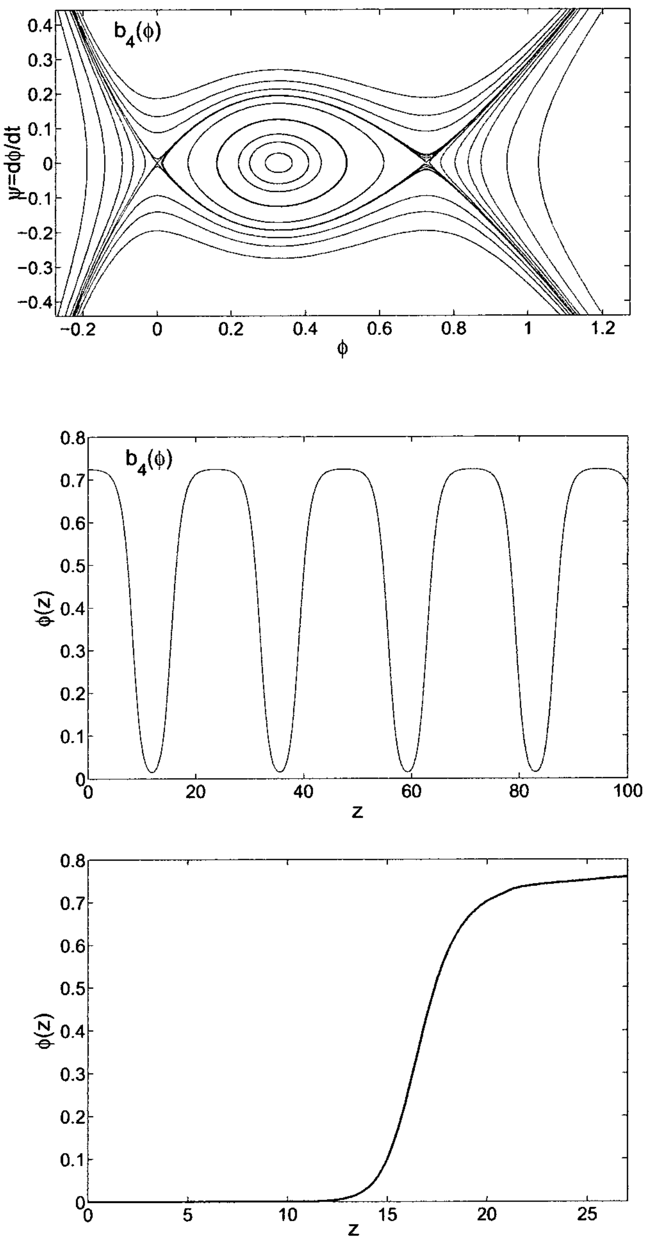


Figure 3.4: Figures from top to bottom represent respectively the phase-plane, a stationary periodic wave and the stationary wavefront when $\alpha = 0$ and $c = 0$.

Chapter 4

Traveling wave solutions

The main goal of the present chapter is to approximate traveling wave solutions of the nonlocal delayed population model. This is of special interest since there appears to be a wide breach between the theoretical and practical work by researchers in the field. Namely, most theoretical works concentrate on the existence and uniqueness of traveling waves and fail to provide any constructive method to obtain the actual wave solutions. On the other hand, several works obtain the wave solution through numerical methods. The numerical wave solutions are mainly dependent on the set of the parameter values and do not capture all characteristics of the wave solution. Hence despite the fact that many of these works are great contributions to the field of mathematical biology, there is a need of constructive methods that can be utilized to obtain the traveling wave solutions.

An accurate approximation of the wave solution enables us to study dynamics of the population in diverse ways. The main advantage of an approximated wave solution compared with a numerical solution is that the former is presented analytically while the latter is valid only for specific parameter values. Hence the elements of wave solution such as frequency, amplitude, period, oscillation or monotonicity can be determined analytically rather than numerically. Also, in this chapter the theoretical results are used to extend some well-known methods to the problem of constructing traveling wave solutions. Then the outcomes of each section are validated with numerical computations.

This chapter is organized as follows. In Section 4.1, existence of slowly traveling wave solutions is numerically investigated. We further examine the oscillatory and monotonic behavior of the traveling wave solutions for the case that there is no delay. In Section 4.2, a boundary layer method is used to obtain approximations of the wave solutions. In Section 4.3, we describe a differential transform method extended to delay differential equations. The method is employed to find approximations of wave solutions. In Section 4.4, some existence results are applied to the case $\alpha = 0$. Then in Section 4.5, an asymptotic method is used to find the wave solution based on the solution for the case $\alpha = 0$. Section 4.6 is a supplement to the monotone iterative method. Finally, in Section 4.7 the velocity of spatial expansion of the population is studied.

4.1 Oscillatory and monotonic waves

Existence of stationary wave pulses and periodic stationary waves were discussed in Chapter 3, Sections 3.2 and 3.3. The first step in the present section is to discuss existence of slowly traveling wave solutions of the population model. Later, we will establish the nonexistence of periodic traveling waves. Also, the oscillatory and non-oscillatory behavior of the wave solution will be studied. In particular, we will numerically demonstrate the behavior of wave for speed $c \geq c^*$ and $c < c^*$, where c^* is the minimal speed.

When $\alpha = 0$ and $\tau = 0$, the wave equation is reduced to the following system of ODEs

$$\begin{cases} \frac{d\phi}{dt} &= \varphi, \\ \frac{d\varphi}{dt} &= \frac{1}{D_m}(c\varphi + f(\phi)), \end{cases} \tag{4.1}$$

where $f(\phi) = d_m\phi - \epsilon b(\phi)$. In Sections 3.2 and 3.3, periodic wave solutions and wave pulses of (4.1) were obtained for $c = 0$ and $b(\phi) = b_i(\phi)$, $i = 1, \cdots, 6$. Here the underlying question is whether the wave solution preserves its periodic or pulse behavior when system (4.1) is slightly perturbed with $0 < c \ll 1$. From Lemma 4 and Lemma 5 we get that a center steady state changes to an unstable spiral when $c = 0$ is slightly increased. This has been numerically presented in Figure 2.5. Further numerical investigation for small values of $c > 0$ did not indicate any periodic behavior. Also the homoclinic orbits vanished where the system was perturbed by $c > 0$. Comparing to the case $c = 0$ (see Figures 3.1-3.3), small values of $c > 0$ result in transformation of periodic stationary wave to oscillatory traveling waves. This has been demonstrated in Figure 4.1. Below are the values of the $c > 0$ and the birth function used in numerical experiments.Top left: $b(\phi) = b_1(\phi), c = 0.002$, top right: $b(\phi) = b_2(\phi), c = 0.01$, bottom left: $b(\phi) = b_3(\phi), c = 0.02$, bottom right: $b(\phi) = b_4(\phi), c = 0.001$.
Let $\psi = [\phi\ \varphi]^T$, $F = \left[\varphi\ \frac{1}{D_m} f(\phi)\right]^T$ and $G = \left[0\ \frac{1}{D_m}\varphi\right]^T$. Then system (4.1) is given by

$$\frac{d\psi}{dt} = F(\psi) + cG(\psi). \tag{4.2}$$

When $c = 0$, system (4.2) has two important properties: first it has a homoclinic orbit at a saddle point. Second, inside the orbit there is a family of periodic orbits. In fact these two properties are the ones required for Melnikov Method [142] to show that the periodic solutions of (4.2) and the homoclinic orbit of (4.2) remain in the phase-plane for $c > 0$ sufficiently small. The only obstacle here that does not allow us to have such a conclusion is the function $G(\psi)$. According to Melnikov Method, $G(\psi)$ must be periodic with respect to t or at least $G(\psi)$ must be depending on a single parameter but theses are not the cases. Also, there is not enough reason to modify $G(\psi)$ in a way that the Melnikov Method becomes applicable. Nevertheless, we thought it is worth mentioning it here.

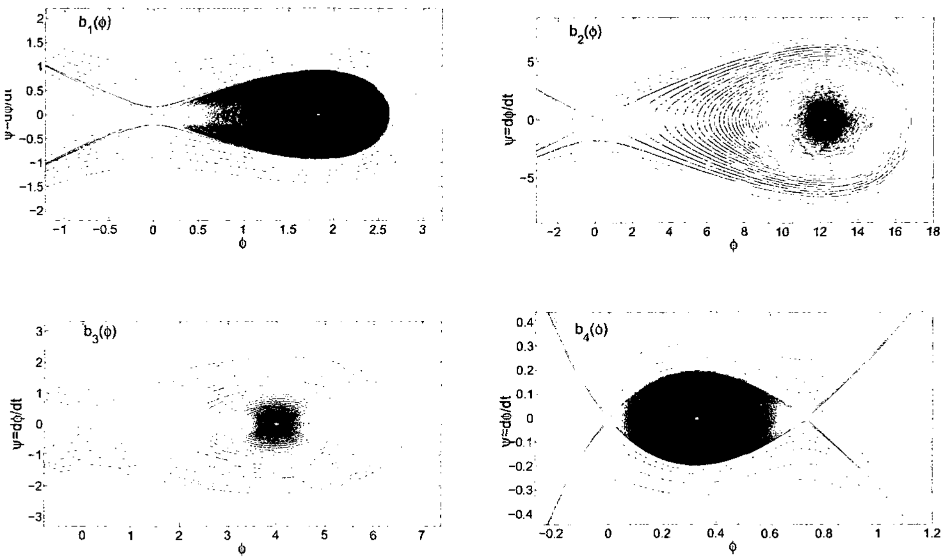


Figure 4.1: phase-plane of the wave equation when $\alpha = 0$ and $c > 0$.

As demonstrated in Section 3.2, Dulac's criteria can be employed to show that the wave equation does not exhibit any periodic behavior. In the following we use the same method to establish nonexistence of periodic traveling wave solutions.

Let $(\phi_1, 0)$ and $(\phi_2, 0)$ be the steady states of (4.1). Consider the following conditions for all $\phi \in (\phi_1, \phi_2)$.

A1) $\left(\frac{3c^2}{D_m} + 2f'(\phi)\right) > 0$

A2) $\frac{8}{D_m}\left(\frac{3c^2}{D_m} + 2f'\right) f^2 > \left(\frac{5c}{D_m} f + f'\right)^2$

Then we have the following proposition.

Proposition 13. Let $\alpha = 0$ and $\tau = 0$. If conditions **A1** and **A2** are satisfied for all $\phi \in (\phi_1, \phi_2)$, then the system (3.10) has no closed orbit in $[\phi_1, \phi_2] \times \mathbb{R}$ and therefore equation (4.1) admits no periodic solution.

Proof.

Let $\rho(\phi,\varphi) = (c\varphi + f(\phi))\varphi$. Using equation (3.13), right-hand sides of (3.10) and considering that $\tau = 0$ we have,

$$\begin{aligned} G(\phi,\varphi) &= 2f'(\phi)\varphi^2 + \tfrac{2}{D_m}(f(\phi)+c\varphi)^2 + f'(\phi) + \tfrac{c}{D_m}(c\varphi + f(\phi))\varphi \\ &= \left(\tfrac{3c^2}{D_m} + 2f'(\phi)\right)\varphi^2 + \left(\tfrac{5c}{D_m}f(\phi) + f'(\phi)\right)\varphi + \tfrac{2}{D_m}f^2(\phi). \end{aligned} \tag{4.3}$$

Condition **A1** implies that $G(\phi,\varphi)$ has the minimum at

$$(\varphi_m, G_m) = \left(\frac{5cf + D_m f'}{-2(3c^2 + 2D_m f')}, \frac{8}{D_m}\left(\frac{3c^2}{D_m} + 2f'\right) f^2 - \left(\frac{5c}{D_m} f + f'\right)^2\right)$$

Condition **A2** implies that $G_m > 0$. Hence for any $\phi \in (\phi_1, \phi_2)$, $G(\phi,\varphi) \geq G_m > 0$. Employing Dulac's criteria (Theorem 11) completes the proof. □

Condition **A1** indicates that the wave speed must be greater than a minimal value to avoid periodic wave solutions. From a general point of view, a necessary condition for monotonicity of a traveling wavefront between steady states ϕ_1 and ϕ_2 is that the wave speed c must be greater than a minimal speed c^*. In Chapter 2 we showed that $c^* = 2\sqrt{D_m(\epsilon p - d_m)}$ for $b(\phi) = b_i(\phi)$, $i = 1,2,3$ (see Lemma 5 and Remark 8). We have numerically confirmed the necessity of the condition $c \geq c^*$.

Figure 4.2 represents the traveling wavefronts of (4.1) with $b(\phi) = b_1(\phi)$ with different values of $c > 0$. The parameter values are as follows. $D_m = 1, d_m = 1, p = 2, \tau = 0, a = 1, \epsilon = 1, q = 1, c = 0.3, 1, 1.5, 2, 2.5.$. Here, $c^* = 2$ and for $c > c^*$ the wavefront is monotonic. Oscillation occurs for values of c less than c^*. Note that the numerical solutions (e.g. Figure 4.2) are obtained with Matlab routine bvp4c.m. Also, the form of the initial guess function plays an important role in obtaining the right solution. For the Figure 4.2 we have used the function $g(t) = \frac{9}{20}(1 + \tanh(t))$ as the initial guess function. Similar results are obtained when birth functions $b_2(\phi)$ or $b_3(\phi)$ are considered. The next section presents a method for approximating the wave solution for the case than mature population diffuses slowly and immature population is immobile.

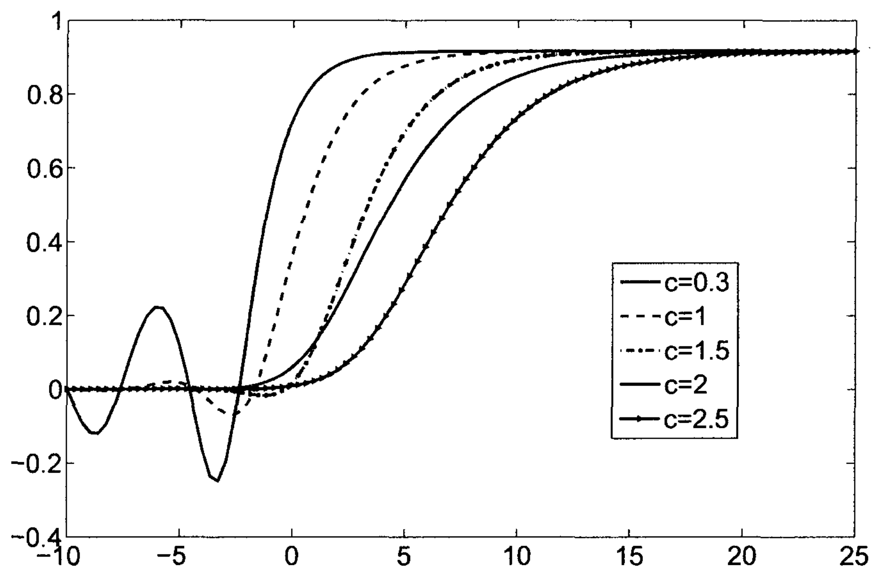


Figure 4.2: Traveling wavefronts of the population model with different values for wave speed c. The wave is monotone when $c \geq c^*$. The birth function is $b(\phi) = b_1(\phi)$; For each plot, the specific value of c is shown in the Figure

4.2 A boundary layer method

The wave equation corresponding to the population model is given by

$$D_m\phi'' - c\phi' - d_m\phi + \epsilon\int_{-\infty}^{\infty} b(\phi(t+y-c\tau))f_\alpha(y)dy = 0. \tag{4.4}$$

In an ecological context, the diffusion coefficient is a measure of the dispersal efficiency of the relevant species. Suppose that the individuals are concentrated at a steady state that is stable in absence of diffusion but loses its stability when diffusion is present. Suppose that for some reason (such as bad environment, decline of food resources, and attack of other species), individuals slowly spread out of that steady state. Then in the framework of our model, we are dealing with the case $D_m = 0$ versus $0 < D_m \ll 1$.

Considering that the propagation of the population in the spatial domain is described by the wave equation (4.4), an approximation of the wave solution gives insights into the local and global behavior of slowly moving individuals. In particular, in this section we will use a boundary-layer method to find an approximation of the traveling wave solution under condition that D_m is very small. A boundary layer is a narrow region where the solution changes rapidly, while in the region outside the boundary layer, the solution changes very slowly. Then the boundary layer region is called inner region and the region of slow variation of solution is called outer region. The main idea behind the boundary layer method is to obtain a leading order approximation to the solution without directly solving the differential equation. This can be done by replacing the original equation with a number of simpler equations that are valid for inner or outer regions.

As before, the wave equation (4.4) is subject to boundary conditions $\lim \phi(t) = \phi_1$ as $t \to -\infty$ and $\lim \phi(t) = \phi_2$ as $t \to \infty$, where ϕ_1 and ϕ_2 are the steady states of (4.4). Assume that the wave solution does not have any heavy tails (i.e. the limits in the boundary conditions tend to ϕ_1 and ϕ_2 fairly fast), then we may replace

$t \to \pm\infty$ in the boundary conditions with $t \to \pm M$, for some $M > 0$ sufficiently large. To be more specific, instead of boundary conditions $\lim_{t\to-\infty} \phi(t) = \phi_1$ and $\lim_{t\to+\infty} \phi(t) = \phi_2$ we may consider $\phi(-M) = \phi_1+\eta$ and $\phi(M) = \phi_2-\eta$ respectively; where $\eta > 0$ is a small constant representing the fact that $\phi(-M)$ and $\phi(+M)$ are not exactly equal to ϕ_1 and ϕ_2 respectively.

According to boundary layer theory, the solution $\phi(t)$ is treated as a function of two independent variables t and D_m. The main goal of the analysis is to find a global approximation to $\phi(t)$ and this can be achieved by performing a local analysis of $\phi(t)$ as $D_m \to 0$. In the wave equation (4.4), the highest order derivative disappears when $D_m = 0$; therefore there is a discontinuity in $\phi(t)$ as $D_m \to 0$. In other words, we are dealing with a singular perturbation problem where the solution $\phi(t)$ for D_m small is not close to the solution of the unperturbed problem (i.e. for $D_m = 0$). Generally speaking, in some regions of domain $t \in [-M, M]$ the solution $\phi(t)$ varies slowly, while there is at least a boundary layer in which the solution varies rapidly.

In the wave equation (4.4) since the coefficient of ϕ' is positive, there is no internal boundary layer (see Section 9.6 of [25]). Specifically, an internal boundary layer appears when there is a change of sign in the coefficient of ϕ'. Nevertheless, we expect that the traveling wave solution $\phi(t)$ changes rapidly inside the domain $t \in (-M, M)$ rather than end points $t = -M$ or $t = M$ (see the numerical approximations carried out in [103]). To overcome such issue we may consider two opposite directions of the traveling wave solution. In fact, by considering $z = x + ct$ and $u(x,t) = \phi(z)$, the wave is described in direction ϕ_1 to ϕ_2 while $z = x - ct$ and $u(x,t) = \phi(z)$ describes the wave in the opposite direction. While equation (4.4) represents the former case, in the latter case, the coefficient of ϕ' is changed to $-c$ and the delay term is replaced with $+c\tau$. In this section we deal with reduced form of the wave equation (i.e when $\alpha = 0$). By taking into account both directions, it is given by,

$$D_m\phi''(t) \pm c\phi'(t) - d_m\phi(t) + \epsilon b(\phi(t \pm c\tau)) = 0, \tag{4.5}$$

where the sign "+" corresponds to $z = x - ct$ and the sign "−" is related to $z = x + ct$. Without any confusion, letter "z" in (4.5) has been replaced with "t". In order to approximate the wave solution, we consider two boundary layer problems: the first deals with equation (4.5) with positive sign on the interval (t^*, M) The second problem is with positive sign on the interval $(-M, t^*)$, where $t^* \in (-M, M)$ is a constant . This has been schematized in Figure 4.3 where the boundary layers are considered to be in the middle (i.e. on the left and right of t^*).

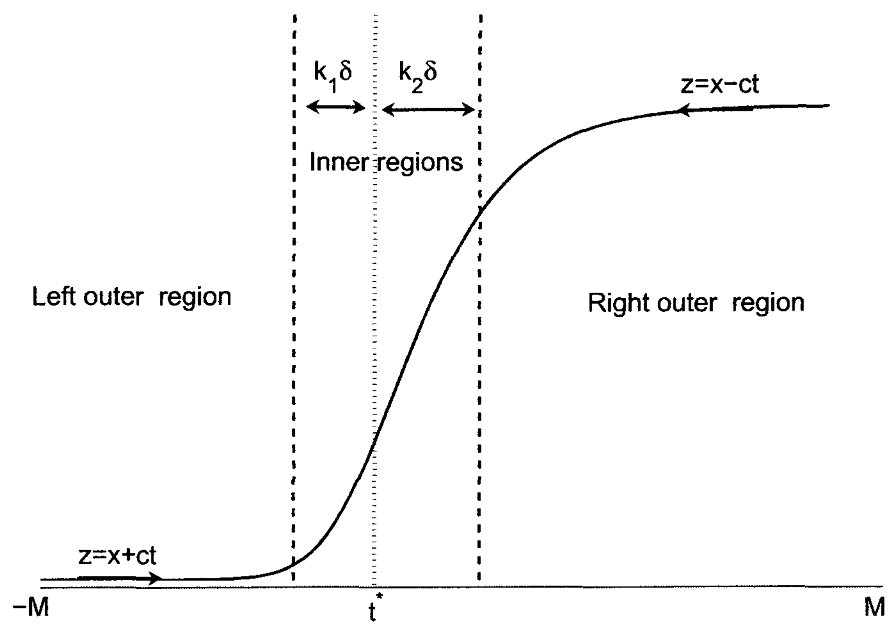


Figure 4.3: A schematic representation of the boundary layer problems. Specifically, the left boundary layer problem corresponds to the equation (4.5) with negative sign and the right boundary layer problem is considered for the positive sign. See the text for more details.

There are two outer regions. Each outer region is characterized by the absence of rapid variation of $\phi(t)$ (i.e. $\phi(t)$, $\phi^{'}(t)$ and $\phi^{''}(t)$ are all of order 1). Let the outer expansion be of the form

$$\phi_{out}(t) = \phi_{out,o}(t) + D_m\phi_{out,1}(t) + \ldots, \text{ as } D_m \to 0. \tag{4.6}$$

Substituting (4.6) into (4.5) gives

$$\pm c\phi^{'}_{out,o}(t) - d_m\phi_{out,o}(t) + \epsilon b(\phi(t \pm c\tau)) = 0. \tag{4.7}$$

Assuming that there is no boundary layer at $t = M$ or $t = -M$, the boundary conditions $\phi_{out,o}(-M) = \phi_1 + \eta$ and $\phi_{out,o}(M) = \phi_2 - \eta$ are imposed onto equation (4.7) with signs "+" and "−" respectively. While the solution of these problems are valid only outside of the boundary layer, we are required to find the corresponding equations inside the boundary layers too. The first step is to specify the thickness δ of the boundary layer based on D_m. The thickness δ can be determined via a dominant-balance argument. The main point is that the solution $\phi(t)$ changes very fast inside each boundary layer. Therefore, to investigate the behavior of the solution, we need to rescale the variable t such that the solution changes regularly rather than fast. In particular, we rescale the t by setting $z = \frac{t-t^*}{\delta}$, $\phi(t) = \phi_{in}(z)$, where t^* is a constant in the interval $(-M, M)$ and it corresponds to the center of a region that the wave solution picks up. Then one may wonder how the value of t^* can be found. The answer lies in the fact that the wave solution has a symmetry in the domain at $(-M, M)$. Depending on the value η in the boundary conditions, we may obtain wave solutions rising at different locations of domain. Hence t^* can be any point in the interval $(-M, M)$.

This has been shown in Figure 4.4 which is a numerical representation of the wave solution $\phi(t)$. Depending on the boundary conditions, the wave solution may rise in different locations. The values in the Figure are the boundary conditions corresponding to each plot. For future purposes we set t^* to a fixed value in the interval $(-M, M)$ such that $\phi(t^*) = \frac{\phi_1+\phi_2}{2}$. This is certainly possible since the

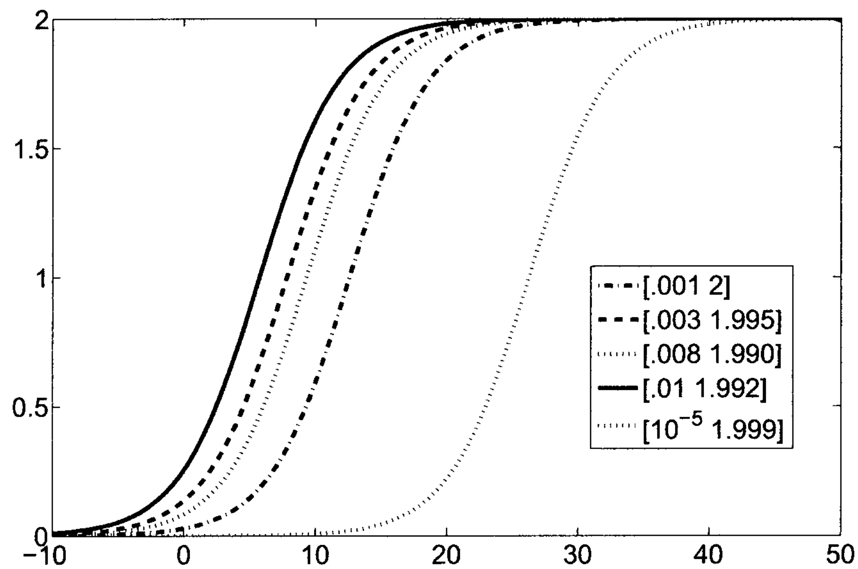


Figure 4.4: A representation of the numerical wave solution. Depending on the boundary conditions, the wave solution may occur in different locations. The values in the Figure are the boundary conditions corresponding to each plot.

wavefront is continuous and it connects ϕ_1 to ϕ_1 in the interval $[-M, M]$. The wave equation inside the boundary layer takes the form,

$$\frac{D_m}{\delta^2}\phi''_{in}(z) \pm \frac{c}{\delta}\phi'_{in}(z) - d_m\phi_{in}(z) + \epsilon b(\phi(z \pm c\tau)) = 0. \tag{4.8}$$

The task is to determine δ based on D_m. There are three possibilities to consider: $\delta(D_m) \ll D_m$, $\delta(D_m) \sim D_m$ and $D_m \ll \delta(D_m)$ as $D_m \to 0$.

In the following we discuss that only the case $\delta(D_m) \sim D_m$ gives a nontrivial boundary-layer matching to outer solution while the other two cases are undistinguished. The first case (i.e. $\delta D_m \ll \delta(D_m)$) implies that only the first terms in (4.8) are dominant. Hence an approximation to (4.8) is given by $\phi''_{in}(z) = 0$ which has the general solution $\phi_{in}(z) = A + Bz$ with A and B as constants. The inner limit does not match the outer solution because $\lim \phi_{in}(z) = \infty$ as $z \to \infty$ unless $B = 0$. But this leads to a contradiction since $\phi_{out}(t^*)$ is finite and not generally equal to A. Similarly the case $D_m \ll \delta(D_m)$ results to an approximation of (4.8) given by $\phi'_{in}(z) = 0$, so $\phi_{in}(z) = A$. Again no match is possible of $\phi_{out}(t^*) \neq A$.
However, the choice $\delta(D_m) \sim kD_m$ gives rise to a distinguished limit since it involves a dominant balance (i.e. a nontrivial relation) between two or more terms of (4.8). Since the boundary layer has thickness $\delta = kD_m$, rescaling the problem by considering $z = \frac{t-t^*}{kD_m}$, $\phi(t) = \phi_{in}(z)$ gives rise to the following dominant balance,

$$\frac{1}{k}\phi''_{in}(z) \pm c\phi'_{in}(z) = kD_m(d_m\phi_{in}(z) - \epsilon b(\phi(z \pm c\tau))). \tag{4.9}$$

Assuming an inner expansion of the form

$$\phi''_{in}(z) = \phi_{in,o}(z) + D_m\phi_{in,1}(z) + \ldots, \tag{4.10}$$

and substituting it into (4.9) gives

$$\frac{1}{k}\phi''_{in,o}(z) \pm c\phi'_{in,o}(z) = 0, \tag{4.11}$$

which has the general solution

$$\phi^{\pm}_{in,o}(z) = A_{\pm} + B_{\pm}e^{\mp kcz}, \tag{4.12}$$

where $A_\pm$ and $B_\pm$ are constants, $\phi^-_{in,o}(z)$ is the approximated wave solution on the right boundary and $\phi^+_{in,o}(z)$ is the one on the left boundary. To find a uniform asymptotic approximation of the wave solution it is necessary to solve (4.7) subject to boundary conditions $\phi_{out,o}(-M) = \phi_1 + \eta$ and $\phi_{out,o}(M) = \phi_2 - \eta$.

The outer region on the left-hand side of the boundary layer (Figure 4.3) is associated with the problem

$$\begin{cases} -c\phi'_{L,o}(t) - d_m\phi_{L,o}(t) + \epsilon b(\phi_{L,o}(t - c\tau)) = 0, \\ \phi_{L,o}(t) = \phi_1 + \eta \text{ for } t \in [-M - c\tau, -M], \end{cases} \tag{4.13}$$

where the subscript L corresponds with the lefthand side outer solution. If the birth function is linear, then using the properties of the Lambert W function equation (4.13) can be directly solved. For instance, let $c = 1$, $\tau = 1$, $d_m = 0$ and $b(\phi) = \phi$. Then for $t > 1$, the solution of (4.13) is given by $\phi_{L,o}(t) = ke^{W(\epsilon)t}$, where k is a constant and W represents Lambert W function. Nevertheless, in most cases, the birth function is nonlinear and the solution has a much more complicated form. In general, the method of steps can be used to solve (4.13). Namely, for the solution $\phi_{L,o}(t)$ in the interval $[-M, M]$, we let $[-M, M] = \bigcup_{k=1}^{n}[-M+(k-1)c\tau, -M+kc\tau]$ where $n = \frac{2M}{c\tau}$ and M is divisible to $c\tau$. Then in the interval $[-M+(k-1)c\tau, -M+kc\tau]$, the delay term in (4.13) is replaced with solution $\phi_{L,o}(t)$ in the interval $[-M+(k-2)c\tau, -M+(k-1)c\tau]$. Thus the problem is reduced to a non-homogeneous first order equation with general solution,

$$\phi_{L,o}(t) = \frac{\epsilon e^{\frac{d_m t}{c}}}{c} \int_{-M+(k-1)c\tau}^{t} e^{-\frac{d_m}{c}s} b(\phi_{L,o}(s - c\tau))ds + re^{\frac{d_m}{c}t}, \tag{4.14}$$

for $t \in [-M + (k-1)c\tau, -M + kc\tau]$, where $r \in \mathbb{R}$ is a constant that is determined from (4.14) by letting $t = -M + (k-1)c\tau$. For instance the solution in the first interval (i.e. $-M \le t \le -M + c\tau$) is given by,

$$\phi_L(t) = \frac{1}{d_m}\left[(d_m(\phi_1 + \eta) - \epsilon b(\phi_1 + \eta))e^{\frac{d_m}{c}(M-t)} + \epsilon b(\phi_1 + \eta)\right]. \tag{4.15}$$

It is important to note that the small perturbation (i.e. the constant η) in the boundary condition plays a crucial role in obtaining the wave solution. If we consider $\eta = 0$, then considering that $b(\phi_1) = 0$ for most of the birth function, the solution of (4.13) is $\phi_L(t) = \phi_1$ for all $t \in [-M, M]$.

Similar to (4.13), for the outer region on the right-hand side, we are required to solve the problem,

$$\begin{cases} c\phi'_{R,o}(t) - d_m\phi_{R,o}(t) + \epsilon b(\phi_{R,o}(t + c\tau)) = 0, \\ \phi_{R,o}(t) = \phi_2 - \eta \text{ for } t \in [M, M + c\tau], \end{cases} \tag{4.16}$$

Let $M - c\tau \leq t \leq M$, then $M \leq t + c\tau \leq M + c\tau$ and delay term in (4.16) is replaced with $\epsilon b(\phi_2 - \eta)$ which is a constant. Therefore similar to the previous case, the problem is reduced to a non-homogeneous first-order differential equation with no delay and the general solution is similar to (4.14).

The next step is to combine the inner and outer solutions into a single uniform asymptotic solution of the form,

$$\phi_{unif}(t) = \begin{cases} \phi_{R,o}(t) + A_+ \quad +B_+e^{-c\frac{t-t^*}{D_m}} - \phi_{R,match}(t) & \text{for } t > t^*, \\ \phi_{L,o}(t) + A_- \quad +B_-e^{c\frac{t-t^*}{D_m}} - \phi_{L,match}(t) & \text{for } t < t^*, \end{cases} \tag{4.17}$$

where $\phi_{L,match}(t)$ and $\phi_{R,match}(t)$ respectively represent the left and right asymptotic matching of the inner and outer solutions. In order to implement the above-mentioned method, consider $b(\phi) = b_2(\phi)$. Then the problems (4.13) and (4.16) can be solved numerically. In particular, the approximated wave solution consists of three parts: $\phi_{L,o}(t), \phi_{in,o}(t)$ and $\phi_{R,o}(t)$. Figure 4.5 represents the outer solutions $\phi_{R,o}(t)$ and $\phi_{L,o}(t)$ in the interval $[-50, 50]$. The specific birth function and parameter values are given below. $b(\phi) = b_2(\phi), d_m = 1, p = 2, a = 1, \tau = 0.3, \epsilon = 1, q = 1, c = 3$. Furthermore, $\eta = .002$ and $M = 50$. Note that the Matlab dde23 does not solve problems of this type. Namely, problem (4.13) starts from $M - c\tau$ and problem (4.16) has a positive lag (i.e. $+c\tau$). To obtain the Figure 4.5 we have used ode45 in a loop of $k = 1$ to $k = n$, where the corresponding non-homogeneous problem

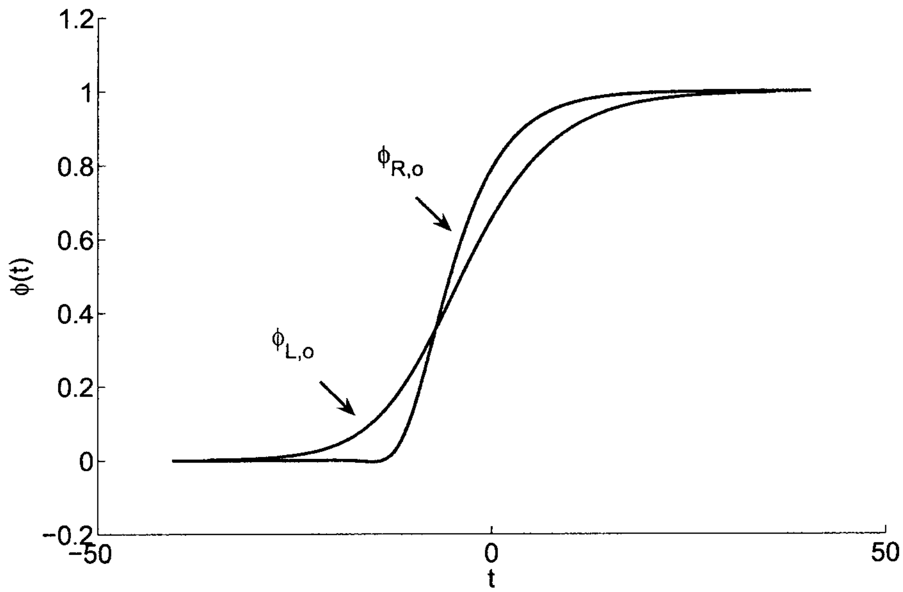


Figure 4.5: outer solutions $\phi_{R,o}(t)$ and $\phi_{L,o}(t)$ in the interval $[-50, 50]$. Also $b(\phi) = b_2(\phi), d_m = 1, p = 2, a = 1, \tau = 0.3, \epsilon = 1, q = 1, c = 3.$, $\eta = .002$ and $M = 50$

is solved in the specified interval of the form $[(k-1)c\tau, kc\tau]$. Using the numerical outcomes for outer solutions, one can assign a value to t^* and choose certain values of the outer solutions to match them with the inner solutions. Namely, we considered $t^* = -7.5$ and inner boundary condition $\phi^{\pm}_{in,o}(t^*) = \frac{\phi_1+\phi_2}{2} = 0.5$. Figure 4.6 represents the approximated wave solution for the inner region for $D_m = 0.1$, $t^* = -7.5$ and $c = 2$. The values of $A_{\pm}$ and $B_{\pm}$ for the equation (4.12) are shown in the Figure.

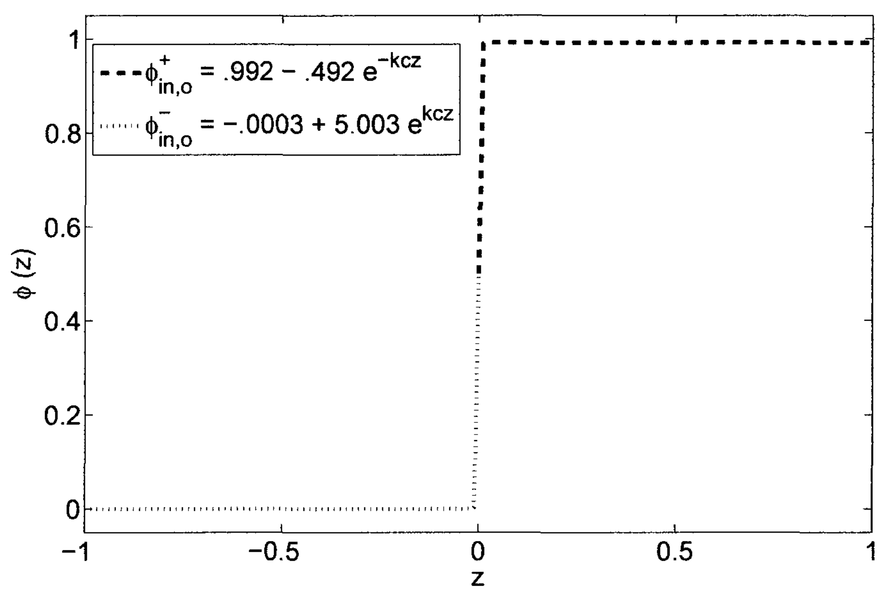


Figure 4.6: The approximated wave solution for the inner region. Here, $D_m = 0.1, z = (t - t^*)/D_m$ with $t^* = -7.5$. The values of $A_{\pm}$ and $B_{\pm}$ are shown in the Figure. See equation (4.12) of the text.

For the asymptotic match of $\phi^{-}_{in,o}(z)$ and $\phi_{L,o}(t)$, we let $\phi_{L,o}(-25) - \phi_{L,macth}(t^*) = 0.9675$. Similarly $\phi^{+}_{in,o}(z)$ and $\phi_{R,o}(t)$ where matched by letting $\phi_{R,o}(10) - \phi_{R,macth}(t^*) = 0.02465$. Figure 4.7 represents the asymptotic uniform solution of the wave equation when $D_m = 0.1$. The vertical lines separate the inner and outer regions.The parameter values are the same as those outlined in the previous Figures.

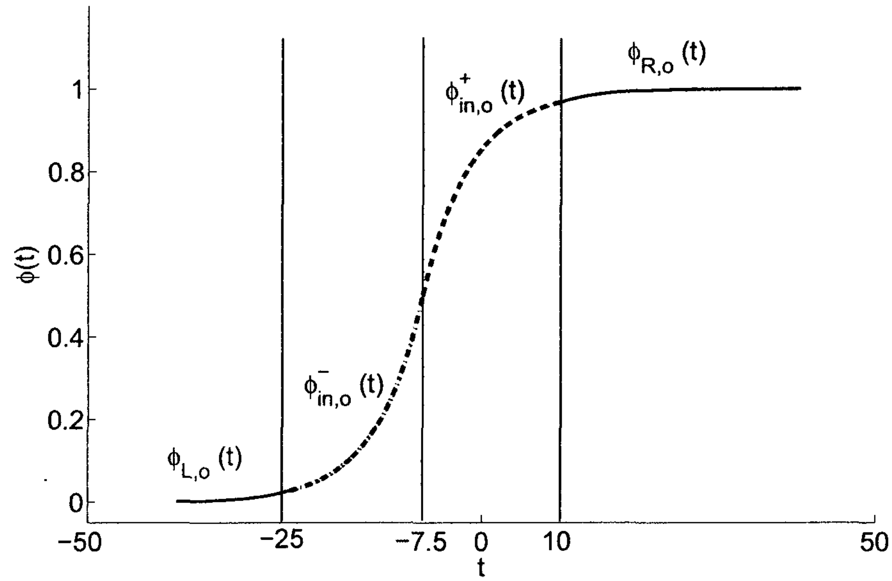


Figure 4.7: An approximation to the traveling wavefront of equation (4.5) obtained by matching the inner and the outer solutions. The approximated wave solution connects the steady state $\phi_1 = 0$ to $\phi_2 = 1$.

Although the uniform asymptotic solution can be obtained through the process described above, the method is challenged with a difficulty. Namely, each outer solution is given in recursive format where the interval close to the boundary layer is obtained only if the solution is calculated in all previous intervals. Hence, despite the fact that we have the explicit forms of the inner solutions, we are missing the explicit forms of the outer solutions. This makes the problem extremely difficult when it comes to matching the inner and outer solutions.

In the next section we apply a new method that does not have such difficulties and the wave solution can be directly approximated through the original wave equation and the related boundary conditions. For the time being let us reduce the problem to a classic boundary layer problem. In particular, by considering $\tau = 0$ the equations in (4.13) and (4.16) are changed to first-order differential equations with no delay. Then considering specific forms of the birth function, the problem can be treated using the classic boundary layer theory. Consider the birth function $b(\phi)$, $b_3(\phi)$ in the form of

$$b_3(\phi) = \begin{cases} p\phi(1 - \frac{\phi^q}{k_c^q}) & 0 \le \phi \le k_c \\ 0 & \phi > k_c, \end{cases} \tag{4.18}$$

with $q = 1$.

We treat the problem as two boundary layer problems. The first problem is when the sign "+" is considered in equation (4.5), while the second problem corresponds to the sign "−". Then the first problem has the domain $t \in [t^*, M]$ with the boundary layer at the lefthand side while the second problem has the domain $t \in [-M, t^*]$ with the boundary layer at the righthand side. The general solution of (4.11) in the boundary layer is given (4.12). Using the boundary conditions $\phi^+_{in,o}(t^*) = (\phi_1 + \phi_2)/2$ and $\phi^-_{in,o}(t^*) = (\phi_1 + \phi_2)/2$, we have

$$\phi^{\pm}_{in,o}(z) = A_{\pm} + (\frac{\phi_1 + \phi_2}{2} - A_{\pm})e^{\mp kcz}, \tag{4.19}$$

When $\tau = 0$ and the birth function is of the form (4.18), equation (4.7) admits the general solution

$$\phi^{\pm}_{out,o}(t) = \frac{K_c(\epsilon p - d_m)}{\epsilon p + s^{\pm} \exp\left(\frac{\epsilon p - d_m}{c}(\pm t - M)\right)}, \tag{4.20}$$

where $s^{\pm}$ are the constants.

Solutions $\phi^{\pm}_{out,o}(t)$ are the outer solutions of the boundary layer problems with respect to the "+" and "−" signs. Then, considering the boundary conditions $\phi^+_{out,o}(-M) = \phi_1 + \eta$ and $\phi^-_{out,o}(M) = \phi_2 - \eta$, the constants s^+ and s^- are determined

$$s^+ = \frac{K_c(\epsilon p - d_m)}{\phi_2 - \eta} - \epsilon p, \tag{4.21}$$

$$s^- = \frac{K_c(\epsilon p - d_m)}{\phi_1 + \eta} - \epsilon p, \tag{4.22}$$

where $\eta > 0$ is a small constant.

Remark 27. The general solution (4.20) is obtained by using the integral formula

$$\int \frac{d\phi}{\phi(a_1 + a_2\phi)} = \frac{1}{a_1} \ln \left| \frac{\phi}{a_1 + a_2\phi} \right| + k, \tag{4.23}$$

where a_1, a_2 and k are constants.

The outer solutions are uniform approximations to the exact solution $\phi(t)$ as $\epsilon \longrightarrow 0^+$ on the subinterval $t^* + \epsilon \ll t \leq M$ and when $\epsilon \longrightarrow 0^-$ on the subinterval $-M \leq t \ll t^* + \epsilon$. More specifically, the difference between the exact solution $\phi(t)$ and the outer solution $\phi^{\pm}_{out}(t)$ is exponentially small as $t \longrightarrow t^*$ and $t \longrightarrow t^*$ until $t - t^* = 0(\epsilon)$. At these two points the outer solutions are already very close to $\phi^{\pm}_{out}(t^*)$ while the actual solution $\phi(t)$ rapidly changes. Then we need to carry out asymptotic matching between the inner and the outer solutions.

For each problem, the asymptotic region occurs on the overlap region which is defined by intermediate limit. For the first problem (i.e. when "+"is considered) an intermediate limit is obtained if, for instance, $t - t^* = \epsilon^{\frac{1}{2}} T$ with $T > 0$ fixed as $\epsilon \longrightarrow 0$. Thus $z \longrightarrow +\infty$ as we go from inner region to outer region. Similarly, for the second problem we have $z \longrightarrow -\infty$. Hence from (4.19) we get that

$$\phi^{\pm}_{in,o}(z) = A_{\pm} \text{ as } x \longrightarrow \pm\infty. \tag{4.24}$$

On the other hand, using (4.20) we get that

$$\lim \phi^{\pm}_{out,o}(t) = \phi^{\pm}_{in,o}(t^*) \text{ as } t \longrightarrow t^{*\pm} \text{ respectively.} \tag{4.25}$$

Matching (4.24) and (4.25) we get that

$$A_{\pm} = \phi^{\pm}_{out,o}(t^*). \tag{4.26}$$

Combining the outer and inner solutions , the uniform approximated wave solution valid for the interval $t \in [-M, M]$ is given by

$$\phi_{unif}(t) = \phi^{\pm}_{out}(t) + \phi^{\pm}_{in}(t) - \phi^{\pm}_{match}(t), \tag{4.27}$$

where the last term represent the asymptotic matching (i. e. $A_{\pm} = \phi^{\pm}_{out}(t^*)$) between the inner and the outer solutions. Hence, the uniform approximated wave solution for $\alpha = 0$, $\tau = 0$ and $b(\phi) = b_3(\phi)$ is given by

$$\phi_{unif}(t) = \begin{cases} \phi^{+}_{out,o}(t) + (\frac{\phi_1+\phi_2}{2} - \phi^{+}_{out,o}(t^*)) \exp(-c\frac{t-t^*}{D_m}) \text{ for } t \geq t^*, \\ \phi^{-}_{out,o}(t) + (\frac{\phi_1+\phi_2}{2} - \phi^{-}_{out,o}(t^*)) \exp(c\frac{t-t^*}{D_m}) \text{ for } t < t^*. \end{cases} \tag{4.28}$$

Figure 4.8 represents a comparison of the exact solution $\phi(t)$ (shown with solid line) and the boundary layer problems with the leading uniform asymptotic approximation $\phi_{unif}(t)$ (shown with dashed line). For this plot $t^* = -7$. The parameter values are $c = 3, K_c = 4, dm = 1, D_m = 0.1, p = 2, \epsilon = 1, \tau = 0$. The steady states are $\phi_1 = 0$ and $\phi_2 = 2$.

We can also compare the outer solutions with the exact solution. Numerical results indicate that the left outer solution is matched with the exact solution and inner solution is vanished. Figure 4.9 represents such a case. It shows that when birth function $b_2(\phi)$ is used the left outer solution takes the same form of the exact solution and the right outer solution remains constant. In this case we have been lucky; there are no boundary layers and the exact solution can be directly approximated with the left outer solution.

Specifically the wave equation (4.5) with $b(\phi) = b_2(\phi)$ has only two steady states: a saddle at ϕ_1 and a node at ϕ_2. Then starting from $\phi_1 + \eta$, the left outer solution has no choice but converging to ϕ_2. This is a special case that a first order differential equation satisfies two boundary conditions. Although the boundary layer approach gives rise to the approximation (4.28) of the wave solution, the problem turns out to be a regular perturbation rather than a singular perturbation. This

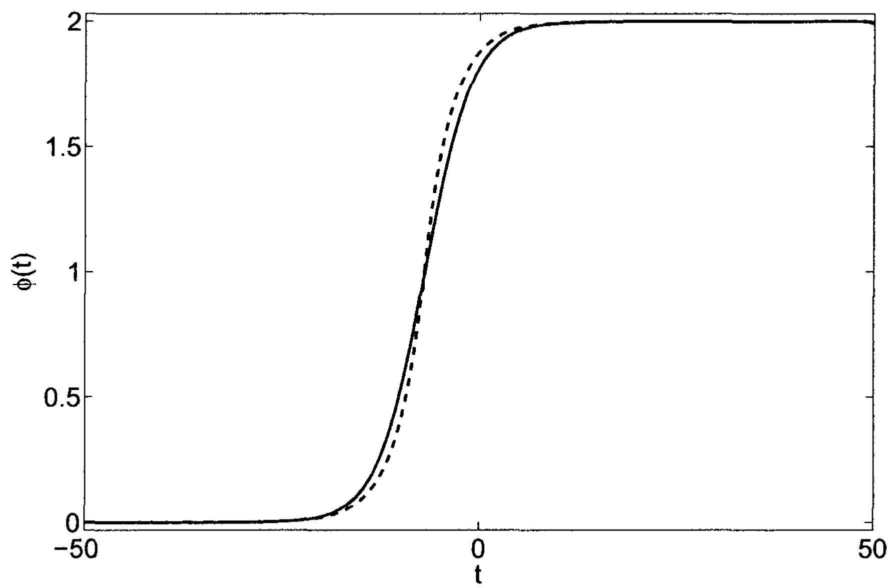


Figure 4.8: A comparison of the exact solution $\phi(t)$ (shown with solid line) to the boundary layer problems with the leading uniform asymptotic approximation $\phi_{unif}(t)$ (shown with dashed line). See the text for the parameter values.

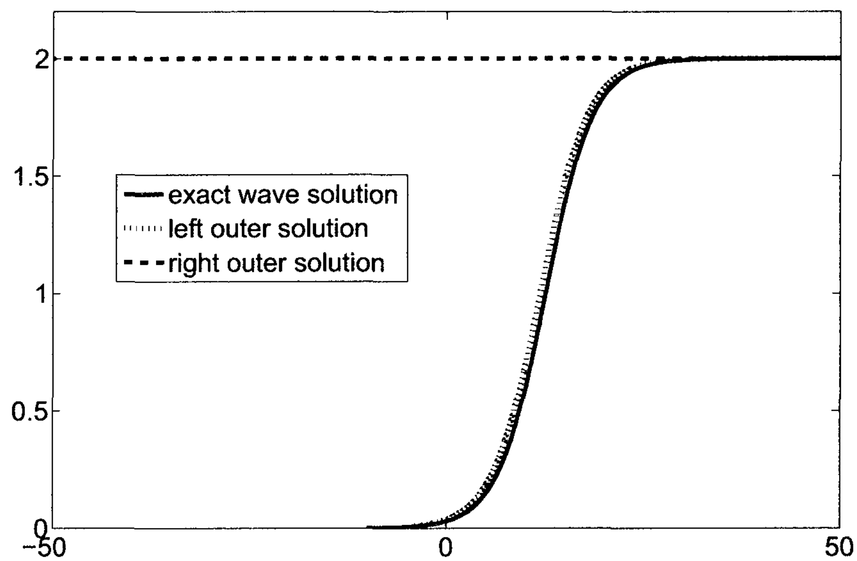


Figure 4.9: A comparison of exact wave solution and the outer solutions. The birth function is $b(\phi) = b_2(\phi)$. The parameter values are given below. $c = 3, K_c = 4, dm = 1, Dm = 0.01, p = 2, \epsilon = 1, \tau = 0$. The steady states are $\phi_1 = 0$ and $\phi_2 = 2$.

means that the solution $\phi^{+}_{out,o}(t)$ in (4.20) is an accurate approximation of the wave solution provided that $D_m \to 0$. Similarly, it can be verified that the wave solution behaves as the outer solution when $b(\phi) = b_i(\phi)$, $i = 1, 2, 5$. This is due to the fact that the wave equation again has only a saddle and a node steady state. let $\epsilon = 1, d_m = 1, a = 1, q = 1$ and $p = 2$, then for $b(\phi) = b_2(\phi)$ and $b(\phi) = b_5(\phi)$ the outer solutions respectively are

$$\phi^{\pm}_{out,o}(t) = \frac{3}{2} \pm \frac{1}{2}(1 + 4\exp(\mp\frac{t + r^{\pm}}{c}))^{\frac{1}{2}} \exp(\pm\frac{t + r^{\pm}}{c}), \tag{4.29}$$

$$\phi^{\pm}_{out,o}(t) = \frac{3}{2} - \frac{1}{2}(1 + 4\exp(\pm\frac{t + r^{\pm}}{c}))^{\frac{1}{2}} \exp(\mp\frac{t + r^{\pm}}{c}), \tag{4.30}$$

where $r^{\pm}$ are constants that are determined by the corresponding boundary conditions.

When $D_m \to 0$, solutions (4.29) and (4.30) are approximations of the exact wave solutions. The actual boundary layer problem occurs when $b(\phi) = b_i(\phi)$, $i = 4, 6$. In this case the wave equation (4.5) has three steady states $\phi_1 = 0, \phi_2$ and ϕ_3. For $c > 2\sqrt{D_m(\epsilon b'(\phi_2) - d_m)}$ there are two saddles with an unstable node between them (see Lemma 5 and Remark 8). Then in this case the boundary layer exists and the wave solution can not be approximated only with the outer solution.

While the approximated wave solutions are an interesting outcome of the boundary layer method, one may note that the method loses its applicability when it comes to more general cases. Namely, when $\tau > 0$ and $\alpha \geq 0$, the explicit form of the approximated wave solution is only available in the inner regions. In Section 4.6 a monotone iterative method is employed to overcome such difficulty.

4.3 Extended differential transform method

In the previous section we made an effort to apply a boundary-layer method for approximation of traveling wave solutions. Despite the fact that the method is applicable to delayed and un-delayed cases, there are some limitations that make the method less practical. Namely, in the presence of delay term $c\tau$, the outer solutions are obtained through the method of steps. The problem is that we do not have the explicit form of the outer solutions. Therefore, the asymptotic matching between the outer and inner solutions becomes problematic. The main goal of this section is to apply a recently developed method to directly solve the wave equation with given boundary conditions. In particular, the Differential Transform Method (DTM) [196] has been recently extended for delay differential equations (DDEs) [82]. Then the solution of the DDEs with discrete delays can be approximated to any desired degree of exactness. We start with some basic definitions.

Definition 7. *The differential transform of a function $\psi(z)$ at a point z_0 is defined as*

$$\Psi(k) = \frac{1}{k!}\left[\frac{d^k}{dz}\psi(z)\right]_{z=z_0}, \tag{4.31}$$

where ψ is analytic at z_0.

Definition 8. *The inverse of the differential transform $\Psi(k)$ is defined by*

$$\psi(z) = \sum_{k=0}^{\infty} \Psi(k)(z-z_0)^k. \tag{4.32}$$

Let the small and capital letters respectively represent the original and transformed functions. Then using (4.31) and (4.32), the following properties can be proven (see [196], [14] and [82]) for the proofs.

1. If $\phi(t) = f(t) \pm g(t)$, then $\Phi(k) = F(k) \pm G(k)$.

2. If $\phi(t) = \gamma f(t)$, then $\Phi(k) = \gamma F(k)$, where γ is a constant.

3. If $\phi(t) = d^n f(t)/dt^n$, then $\Phi(k) = [(k+n)!/k!]\, F(k+n)$.

4. If $\phi(t) = f(t)g(t)$, then $\Phi(k) = \sum_{k_1=0}^{k} \begin{pmatrix} k \\ k_1 \end{pmatrix} F(k_1)G(k-k_1)$.

5. If $\phi(t) = f(t+a)$, then $\Phi(k) = \sum_{h_1=k}^{N} \begin{pmatrix} h_1 \\ k \end{pmatrix} a^{h_1-k}F(h_1)$ for $N \to \infty$, where

$$\begin{pmatrix} h_1 \\ k \end{pmatrix} = \frac{h_1!}{(h_1-k)!k!}$$

In the following we will demonstrate how the extended DTM can be applied to solve the wave equation with the boundary conditions. We consider the case that $\alpha = 0$. In an ecological sense, this corresponds to the case that the immature population has no mobility and they remain concentrated at the steady state. There have been several studies devoted to this case. For instance, in [119], Hopf bifurcation theory and some numerical methods have been applied to study the wave solutions under parameter changes.

For $M > 0$ sufficiently large, we may replace the original boundary conditions with their approximations. Specifically, the wave equation with the boundary conditions is given by

$$\begin{cases} D_m\phi''(t) - c\phi'(t) - d_m\phi(t) & +\epsilon b_i(\phi(t-c\tau)) = 0, \\ \phi(-M) = \phi_1, & \phi(M) = \phi_2, \end{cases} \tag{4.33}$$

where ϕ_1 and ϕ_2 are the steady states of the wave equation.

A major benefit of the extended DTM is that the method does not require the history function. Similar to boundary value problems in ODEs, we only require the actual equation and the boundary conditions.

By rescaling the problem, $-M$ and M are transformed to 0 and 1. In particular, let

$z = \frac{1}{2}(\frac{t}{M} + 1)$ and $\psi(z) = \phi(t)$ then the wave equation (4.33) is transformed to

$$\begin{cases} D_m\psi''(t) - 2cM\psi'(z) - 4d_mM^2\psi(z) & +4\epsilon M^2 b_i(\psi(z - \frac{c\tau}{2M})) = 0, \\ \psi(0) = \phi_1, & \phi(1) = \phi_2. \end{cases} \tag{4.34}$$

To apply the extended DTM it is required to know the specific form of the birth function. Let us consider the birth function $b_3(\psi)$ with $q = 1$ that is given by

$$b_3(\psi) = \begin{cases} p\psi(1 - \frac{\psi}{k_c}) & 0 \leq \psi \leq k_c \\ 0 & \psi > k_c, \end{cases}$$

For our specific problem, more properties of differential transforms are needed. We add the following Theorem to the newly developed theory of differential transforms.

Theorem 12. The differential transform of $\phi(t) = f_1(t + a)f_2(t + b)$ with $a, b \in \mathbb{R}$ is given by

$$\Phi(k) = \lim \sum_{k_1=0}^{k} \sum_{h_1=k}^{N} \sum_{h_2=k-k_1}^{N} \begin{pmatrix} h_1 \\ k_1 \end{pmatrix} \begin{pmatrix} h_2 \\ k - k_1 \end{pmatrix} a^{h_1-k} b^{h_2-k+k_1} F_1(h_1)F_2(h_2), \tag{4.35}$$

for $N \to \infty$.

Proof.

Let the differential transforms of $f_1(t+a)$ and $f_2(t+b)$ at $t = t_0$ be $F_1(k)$ and $F_2(k)$ respectively. By using the property (4) we have the differential transform of $\phi(t)$ as

$$\Phi(k) = \sum_{k_1=0}^{k} F_1(k_1)F_2(k - k_1). \tag{4.36}$$

From property (5) we get

$$F_1(k) = \sum_{h_1=k_1}^{N} \begin{pmatrix} h_1 \\ k_1 \end{pmatrix} a^{h_1-k_1} F_1(h_1) \text{ for } N \to \infty. \tag{4.37}$$

Similarly,

$$F_2(k - k_1) = \sum_{h_2=k-k_1}^{N} \begin{pmatrix} h_2 \\ k - k_1 \end{pmatrix} b^{h_2-k+k_1} F_2(h_2) \text{ for } N \to \infty. \tag{4.38}$$

The proof is completed by substituting (4.37) and (4.38) into (4.36). $\square$

Using the properties (1)-(5) and Theorem 12, the differential transform of problem (4.34) is given by

$$
\begin{gathered}
D_m(k+2)(k+1)\Psi(k+2) - 2cM(k+1)\Psi(k+1) - \\
4d_m M^2\Psi(k) + 4\epsilon p M^2 \sum_{h_1=k}^{N} \begin{pmatrix} h_1 \\ k \end{pmatrix} (-c\tau)^{h_1-k}\Psi(h_1) - \\
\frac{\epsilon p M^2}{k_c} \sum_{k_1=0}^{k} \sum_{h_1=k_1}^{N} \sum_{h_2=k-k_1}^{N} \begin{pmatrix} h_1 \\ k_1 \end{pmatrix} \begin{pmatrix} h_2 \\ k-k_1 \end{pmatrix} (-c\tau)^{h_1+h_2-k}\Psi(h_1)\psi(h_2) = 0,
\end{gathered}
\tag{4.39}
$$

for $N \to \infty$ and subject to the boundary conditions $\psi(0) = \phi_1$ and $\psi(1) = \phi_2$.

By letting $N = M < \infty$, $k = 0, 1, \ldots, M-2$ and using the boundary conditions, equation (4.39) corresponds to a homogeneous nonlinear system of equations with $M-1$ unknowns (i.e. $\Phi(k)$ for $k = 2, \ldots, M$) and $M-1$ equations. Then using symbolic computation software such as Maple, the nonlinear system can be solved. Noting that the solution may not be unique, it is necessary to use the existing theory of traveling waves to exclude the ill-behaved solutions.

Namely, we are looking for a traveling wavefront that is monotonic and satisfies the boundary conditions. Here, after finding all possible solution sets $\{\Phi(k)\}_{k=0}^{M}$, each set is plugged into equation (4.32) with $z_0 = 0$ and the desired approximated wave solution is found.

In a broad context, the above mentioned approach provides a basis to implement techniques of solving nonlinear homogeneous systems for finding approximations of the wave solutions. We are currently attempting to accomplish this goal.

4.4 Some existence results

Existence of traveling and stationary wavefronts is equivalent to existence of heteroclinic orbits in the phase-plane. In Sections 3.3 and 3.4 of Chapter 3 we obtained the analytic forms of the homoclinic and heteroclinic orbits of stationary waves. We also investigated the existence and non-existence of periodic orbits. The present section deals with heteroclinic orbits corresponding to the stationary and traveling wavefronts. Fortunately, some existence results published in mathematical journals can be directly applied to the cases that are considered below.

We start with the case that immature individuals are non-diffusive (i.e. $\alpha = 0$) and the system is independent of any delay (i.e. $\tau = 0$). Then the corresponding wave equation with boundary conditions is given by,

$$\begin{cases} \phi'' = h(\phi, \phi') & , \\ \phi(-\infty) = \phi_1, \quad \phi(+\infty) = \phi_2, \end{cases} \tag{4.40}$$

where ϕ_1 and ϕ_2 are the steady states of the wave equation and $h(\phi, \phi') = \frac{1}{D_m}(c\phi' + d_m\phi - \epsilon b(\phi))$.

Let $\phi_1 = 0$ and $\phi_2 > 0$. Assume there exists a constant $L > 0$ such that either

$$\textbf{H1)} \begin{cases} h(\phi, 0) < 0 & \text{for all } \phi \in (0, \phi_2), \\ h(\phi, \phi') \geq \phi_2\sqrt{L}(2\phi' - \sqrt{L}\phi), & \text{for all } (\phi, \phi') \in [\phi_1, \phi_2] \times [0, \infty)\ , \end{cases}$$

or

$$\textbf{H2)} \begin{cases} h(\phi, 0) > 0 & \text{for all } \phi \in (0, \phi_2), \\ h(\phi, \phi') \leq \phi_2\sqrt{L}(-2\phi' + \sqrt{L}(1 - \phi)), & \text{for all } (\phi, \phi') \in [\phi_1, \phi_2] \times [0, \infty)\ . \end{cases}$$

The following theorem is a direct implication of the theorem given by Malaguti & Marcelli [117].

Theorem 13. Assume there exists a constant $L > 0$ such that either **H1** or **H2** holds. Then (4.40) has a strictly monotone solution.

Proof.

By rescaling the problem (4.40) to $\phi = \phi_2\hat{\phi}$ and rewriting the problem based on

$\hat{\phi}$, the boundary conditions are changed to $\hat{\phi}(-\infty) = 0$ and $\hat{\phi}(+\infty) = 1$. Using Theorem A of Malaguti & Marcelli [117] completes the proof. □

Remark 28. By Theorem 13 existence of monotone traveling wavefronts is implied when condition **H1** or **H2** is satisfied.

Remark 29. From Lemma 5 and remark 8 of Chapter 2 we get that for $c^2 < 4D_m(\epsilon b(\phi_j) - d_m))$ the problem (4.40) cannot have any monotone solution and therefore conditions **H1** or **H2** cannot be satisfied.

In the case that delay is present (i.e. $\tau > 0$), the boundary value problem is given by

$$\begin{cases} D_m\phi''(t) - c\phi'(t) - d_m\phi(t) + \epsilon b(\phi(t - c\tau)) = 0, \\ \phi(-\infty) = \phi_1, \ \phi(+\infty) = \phi_2. \end{cases} \tag{4.41}$$

The work by Faria & Trofimchuk [45] shows that traveling wavefronts of (4.41) exist if the equation

$$\phi'(t) = -d_m\phi(t) + \epsilon b(\phi(t)) \tag{4.42}$$

has a heteroclinic solution connecting $\phi_1 = 0$ to ϕ_2 and the following conditions **A1** - **A6** (**A$'$6**) are satisfied.

A1) $b(\phi)$ is continuous and C^1 in a neighborhood of zero, $b(0) = 0$, $b(\phi) > 0$ for all $\phi > 0$, $\lim_{\phi\to\infty} b(\phi) = 0$. There is $\phi_M > 0$ such that $b(\phi)$ is strictly increasing on $(0, \phi_M)$ and strictly decreasing on (ϕ_M, ∞).

A2) ϕ_2 is the only positive steady state of (4.41) and $\phi_2 > \phi_M$.

A3) $\epsilon b'(0) > d_m$ and $b(\phi) \leq b'(0)\phi$ for ϕ in the neighborhood $[0, v]$ for some $v > 0$.

A4) In equation (4.42), $\phi_2 > 0$ is asymptotically stable.

A5) In equation (4.42), $\phi_1 = 0$ is unstable such that all corresponding eigenvalues have non-zero real parts and there are $M \geq 1$ eigenvalues with positive real parts.

A6) There is a heteroclinic solution for (4.42) connecting ϕ_1 to ϕ_2.

Faria and Trofimchuk show [45] that condition A6 is satisfied if

A$^{'}$6) In equation (4.42), ϕ_2 is globally attractive in the set of all positive solutions.

In particular under the following conditions the set of all traveling wave solutions of (4.41) forms a C^1-smooth M-dimensional manifold in some $C_b(\mathbb{R}, \mathbb{R})$-neighborhood of the heteroclinic solution of (4.42) (see Theorems 1 and 12 of [45]).

The characteristic equation obtained by linearizing (4.42) about $\phi = \phi_j$ for $j = 1, 2$ is given by

$$\lambda + d_m - \epsilon b^{'}(\phi_j)e^{-\tau\lambda} = 0. \tag{4.43}$$

When $c = 1$ or $\tau = 0$, the local stabilities of ϕ_1 and ϕ_2 of (4.42) are the same as those of the model (2.7). This is due to the fact that when $c = 1$ or $\tau = 0$, the equation (4.43) is the same as the characteristic equation related to the model (2.7). In the case that $\tau = 0$ and $b(\phi) = b_i(\phi)$ for $i = 1, \ldots, 6$, the stability results given in Lemma 2 are the same for both equations (4.43) and (2.7).

Remark 30. Following the same argument given in the proof of Theorem 3 it can be shown that stability of ϕ_1 and ϕ_2 of (4.42) are independent of delay τ when $\epsilon|b(\phi_j)| < d_m$, $j = 1, 2$.

Remark 31. From Corollary 1 and the remark above, we get that the local stability of ϕ_1, ϕ_2 and ϕ_3 of (4.42) with $b(\phi) = b_i(\phi)$, $i = 1, \ldots, 6$ is the same as those outlined in Table 2.2

Fortunately the birth functions b_1, b_2 and b_3 and the corresponding steady states ϕ_1 and ϕ_2 have the capability of satisfying all conditions **A1-A6** (**A$^{'}$6**) . In particular the following theorem is an implication of Theorem 12 in [45].

Theorem 14. Let the birth function $b(\phi) = b_i(\phi)$, $i = 1, 2, 3$. Let $\frac{\epsilon p}{d_m} > 1$. Assume that 1) $\tau \neq \tau_n$ where $\tau_n = \frac{2n\pi - \arccos\left(\frac{d_m}{\epsilon p}\right)}{\sqrt{(\epsilon p)^2 - d_m^2}}$, $n \in \mathbb{N}$ 2) $\tau < \hat{\tau}$, where $\hat{\tau}$ is defined in (2.34)

3) ϕ_2 is globally attractive; then for $c > 0$ sufficiently large, (4.41) has a traveling wave solution of speed c, connecting ϕ_1 to ϕ_2.

Proof.

It is easy to verify the conditions **A1-A3**. Also when $b(\phi) = b_i(\phi)$, $i = 1, 2, 3$ by Lemma 2, ϕ_2 is asymptotically stable. Since $\frac{\epsilon p}{d_m} > 1$ and $\tau \neq \tau_n$, ϕ_1 is unstable and hyperbolic. Then one can see that conditions **A5** and **A$'$6** are also satisfied. Using Theorem 12 of [45], the result is obtained. $\square$

The next section employs the results of this section to obtain the traveling wave solution for the case $0 < \alpha \ll 1$ based on a wave solution of the case $\alpha = 0$.

4.5 An asymptotic expansion method

The aim of this section is to investigate traveling wave solutions of the general population model when $0 < \alpha \ll 1$. This corresponds to the case that the immature population diffuses very slowly in the spatial domain. In the previous section we discussed some existence results for the case that $\alpha = 0$. Assume that the wave solution $\phi_0(t)$ of the wave equation with $\alpha = 0$ is known. Then, our goal in this section is to find an approximation of the wave solution based on $\phi_0(t)$.

Define the weighted average of the birth function $b(\phi)$ in the form of the convolution

$$(f_\alpha * b)(\phi) := \int_{-\infty}^{\infty} b(\phi(t + y - c\tau)) f_\alpha(y) dy. \tag{4.44}$$

The wave equation (2.8) is rewritten as

$$D_m \phi'' - c\phi' - d_m \phi + \epsilon (f_\alpha * b)(\phi) = 0. \tag{4.45}$$

We note that $f_\alpha(y) = \frac{1}{\sqrt{4\pi\alpha}} e^{\frac{-y^2}{4\alpha}}$ is a probability density function defined on $(-\infty, \infty)$ that has the property

$$f_\alpha * 1 = 1. \tag{4.46}$$

Furthermore, the average A of ϕ is given by

$$A := (f_\alpha * I)(\phi) = \phi - m, \tag{4.47}$$

where $I(\phi) = \phi$ and m is the mean or centroid of f_α such that

$$m := \int_{-\infty}^{\infty} y f_\alpha(y) dy. \tag{4.48}$$

The variance of $f_\alpha(y)$ is defined as

$$v := \int_{-\infty}^{\infty} (y - m)^2 f_\alpha(y) dy. \tag{4.49}$$

With specific form of $f_\alpha(y)$ mentioned above, the mean and variance are calculated as follows:

$$m = \frac{1}{\sqrt{4\pi\alpha}} \int_{-\infty}^{\infty} y e^{\frac{-y^2}{4\alpha}} = \frac{-2\alpha}{4\pi\alpha} e^{\frac{-y^2}{4\alpha}} \Big]_{-\infty}^{\infty} = 0, \tag{4.50}$$

$$\begin{aligned} v &= \tfrac{1}{\sqrt{4\pi\alpha}} \textstyle\int_{-\infty}^{\infty} y^2 e^{\frac{-y^2}{4\alpha}}, \\ &= \tfrac{1}{\sqrt{4\pi\alpha}} \left(-2\alpha y e^{\frac{-y^2}{4\alpha}}\right]_{-\infty}^{\infty} + 2\alpha \textstyle\int_{-\infty}^{\infty} e^{\frac{-y^2}{4\alpha}} dy), \\ &= 2\alpha. \end{aligned} \tag{4.51}$$

Here, the main idea is to replace the convolution term in (4.45) with a simpler form. Then the approximated wave equation can be solved and the solution can be expressed based on the solution of the case $\alpha = 0$. When there is no convolution (i.e. when $\epsilon = 0$), the wave equation (4.45) is reduced to a linear oscillator with negative damping and stiffness. An equation of this type has been well-studied in various physical systems (see for example [176]). The negative damping is due to $d_m > 0$ which makes the system unstable at origin. The physical interpretation of instability at origin is that the energy will not be lost due to friction or resistance; instead it will be generated within the system. Therefore, a slight disturbance of the origin results in the solution $\phi(t)$ being carried away from the origin. The negative stiffness is due to $c > 0$ which makes the origin a saddle steady state rather that an unstable node or spiral.

When $\epsilon > 0$ the equation (4.45) represents a linear oscillator with a delayed nonlinear damping. Solving the integral equations involved with delay terms is not an easy task; nevertheless, certain conditions may permit for Taylor expansion of the birth function $b(\phi)$ and reduction of the convolution term to a simpler form. There is a general formula known as Watson's Lemma (see Chapter 4 of [42]), which gives the full asymptotic expansion of the integral

$$I(\xi) = \int_0^\gamma g(z)e^{-\xi z}dz, \gamma > 0 \text{ as } \xi \to +\infty. \tag{4.52}$$

In particular, if $g(z)$ is continuous on $z \in [0, \gamma]$ and it has the asymptotic expansion

$$g(z) \sim z^\theta \sum_{n=0}^{\infty} a_n z^{\beta n}, z \to 0^+, \tag{4.53}$$

with $\theta > -1$ and $\beta > 0$, then we have

$$I(\xi) \sim \sum_{n=0}^{\infty} \frac{a_n \Gamma(\theta + \beta n + 1)}{\xi^{\theta+\beta n+1}}, \xi \to +\infty. \tag{4.54}$$

Note that if $\gamma = \infty$, then for convergence of $I(x)$ we need $g(z) \ll e^{\eta z}(z \to \infty)$ for some positive constant $\eta > 0$. The proof of (4.54) is given on page 264 of [25].
Let $\xi = \frac{1}{4\alpha}$, $z = y^2$ and $g_\pm(z) = \frac{b(\phi(t\pm\sqrt{z}-c\tau))}{\pm\sqrt{z}}$. Then the convolution is rewritten as

$$(f_\alpha * b)(\phi) = \sqrt{\frac{\xi}{4\pi}}(I_+(\xi) + I_-(\xi)), \tag{4.55}$$

where the signs + and - correspond to functions g_+ and g_- respectively. Although Watson's Lemma provides a good approximation for the convolution, there are two major issues with this approach. First $g_\pm(z)$ is involved with the wave solution $\phi(t)$ and there is no way to check whether or not the condition (4.53) is satisfied for $g_+(z)$ and $g_-(z)$. We may assume that (4.53) is satisfied and later show that such assumption is true. Even though, the second issue confines us to seek for another path. Namely, replacing the convolution with the approximations of the form (4.54) does not seem to make the wave equation (4.45) easier to solve. We may take the second approach described below. The generalized form of the Watson's Lemma deals with integrals of the form

$$I(\xi) = \int_{\gamma_1}^{\gamma_2} g(z)e^{\xi r(z)}dz, \tag{4.56}$$

where $r(z)$ is a known function of z.

Although it might be useful to make a change of variable and rewrite the integral (4.56), we try to obtain the leading behavior of $I(\xi)$ as $\xi \to \infty$. In particular, when $r(z)$ has a maximum at $z = M \in (\gamma_1, \gamma_2)$ we can approximate $I(\xi)$ by

$$I(\xi, \nu) = \int_{M-\nu}^{M+\nu} g(z)e^{\xi r(z)}dz, \tag{4.57}$$

This can be verified by integration by parts and showing that $I(\xi) - I(\xi, \nu)$ is subdominant as $\xi \to \infty$ (see [25] for more details).

Then in the narrow region $|z - M| \le \nu$, $r(z)$ can be replaced by the first few terms of its Taylor series. We also expand $g(z)$ about $z = M$. We get that

$$I(\xi, \nu) \sim \int_{M-\nu}^{M+\nu} \hat{g}_{k_1}(z)e^{\xi \hat{r}_{k_2}(z)}dz, \xi \to \infty, \tag{4.58}$$

where $\hat{g}_{k_1}(z)$ and $\hat{r}_{k_2}(z)$ are Taylor expansions with terms truncated at orders k_1 and k_2 respectively.

Since for all z on the interval $\gamma_1 \le z \le M - \nu$ and $M + \nu \le z \le \gamma_2$, $e^{\xi r(z)}$ is exponentially smaller than $e^{\xi r(M)}$ as $\xi \to \infty$, then the expression

$$\left|\int_{\gamma_1}^{M-\nu} g(z)e^{\xi r(z)}dz\right| + \left|\int_{M+\nu}^{\gamma_2} g(z)e^{\xi r(z)}dz\right|$$

is subdominant with respect to $I(\xi)$ as $\xi \to \infty$. By letting $\gamma_1 = -\infty$ and $\gamma_2 = +\infty$, with the above explanation and (4.58), we get that

$$I(\xi) \sim \lim_{\nu \to \infty} I(\xi, \nu) \sim \int_{-\infty}^{\infty} \hat{g}_{k_1}(z)e^{\xi \hat{r}_{k_2}(z)}, \xi \to \infty. \tag{4.59}$$

Let $z = y$, $r(z) = \frac{-z^2}{4}$, $\xi = \frac{1}{\alpha}$ and $g(z) = b(\phi(t + z - c\tau))$. Then the convolution (4.44) is given by

$$(f_\alpha * b)(\phi) = \sqrt{\frac{\xi}{4\pi}} I(\xi). \tag{4.60}$$

Since $r(z)$ has a maximum at $z = 0$ from (4.59) we get that

$$(f_\alpha * b)(\phi) \sim \sqrt{\frac{\xi}{4\pi}} \int_{-\infty}^{\infty} \hat{g}_{k_1}(z) e^{\xi \hat{r}_{k_2}(z)}, \xi \to \infty. \tag{4.61}$$

In other words, when $\alpha \to 0$, the convolution (4.44) can be approximated by replacing $b(\phi(t + y - c\tau))$ with its Taylor expansion about zero. This is given by

$$b(\phi(t + y - c\tau)) = b(\phi(t - c\tau)) + b^{(1)}(t - c\tau)y + \frac{1}{2}b^{(2)}(t - c\tau)y^2 + O(y^3), \tag{4.62}$$

where

$$b^{(1)}(t - c\tau) = b^{'}(\phi)\phi^{'}(s)_{s=t-c\tau} \tag{4.63}$$

$$b^{(2)}(t - c\tau) = \phi^{'2}(s)b^{''}(\phi) + \phi^{''}(s)b^{'}(\phi)_{s=t-c\tau} \tag{4.64}$$

Substituting (4.62) into (4.44) and noting that b, $b^{(1)}$ and $b^{(2)}$ are independent of the variable y, we use (4.46), the mean and the variance calculated in (4.50) and (4.51) to obtain the following approximation of the convolution

$$(f_\alpha * b)(\phi) \sim b(\phi(t - c\tau)) + \alpha b^{(2)}(t - c\tau) \text{ as } \alpha \to 0. \tag{4.65}$$

We conclude that the wave equation is approximated by

$$D_m\phi^{''}(t) - c\phi^{'}(t) - d_m\phi(t) + \epsilon b(\phi(t - c\tau)) + \epsilon\alpha b^{(2)}(t - c\tau) = 0, \tag{4.66}$$

provided $\alpha \to 0$.

In the previous section we have discussed existence of traveling wavefronts of the reduced wave equation (i.e. when $\alpha = 0$). equation (4.66) shows that small values of α slightly perturb the reduced wave equation with the term $\epsilon\alpha b^{(2)}(t - c\tau)$. Hence a perturbation analysis can be used to obtain approximations of the wave solution. Let

$$\phi(t) = \phi_0(t) + \alpha\phi_I(t) + \alpha^2\phi_{II}(t) + \cdots \tag{4.67}$$

Substituting (4.67) into (4.66) we find that $\phi_0(t)$ is the solution of the reduced wave equation. Moreover, using (4.64), $\phi_I(t)$ satisfies the following equation

$$D_m\phi_I''(t) + c\phi_I'(t) - d_m\phi_I(t) + \epsilon h(\phi_0(t - c\tau)) = 0, \tag{4.68}$$

where

$$h(\phi_0(t - c\tau)) = b''(\phi_0(t - c\tau)\phi_0'^2(t - c\tau) + b'(\phi_0(t - c\tau))\phi_0''(t - c\tau). \tag{4.69}$$

Noting that ϕ_0 is the known solution, equation (4.68) is a non-homogeneous second order differential equation that can be solved by using standard methods. Namely, the solution of (4.68) is presented below.

$$\phi_I(t) = \frac{\epsilon}{D_m(\beta_2 - \beta_1)}\left[\int_{-\infty}^{t} e^{\beta_1(t-s)}h(\phi_0(s - c\tau))ds + \int_{t}^{\infty} e^{\beta_2(t-s)}h(\phi_0(s - c\tau)ds\right], \tag{4.70}$$

where $t \in \mathbb{R}$, $\beta_1 = \frac{c-\sqrt{c^2+4D_md_m}}{2D_m}$ and $\beta_2 = \frac{c+\sqrt{c^2+4D_md_m}}{2D_m}$.

We conclude that when $0 < \alpha \ll 1$ and $\phi_0(t)$ is known, the wave solution is approximated by

$$\phi(t) \sim \phi_0(t) + \alpha\phi_I(t), \tag{4.71}$$

provided $\alpha \longrightarrow 0$.

The main outcome of the present section is that the wave solution of the case $0 < \alpha \ll 1$ is expressed based on the solution of the case $\alpha = 0$. Hence, using the outcomes of the Sections 4.2 and 4.3, the wave solution is approximated. For instance, when $b(\phi) = b_3(\phi)$ the approximated wave solution is given by

$$\phi_{approx}(t) = \phi^+_{out,0}(t) + \alpha\phi_I(t),$$

provided that $\alpha \longrightarrow 0$ and $D_m \longrightarrow 0$. Note that $\phi^+_{out,0}(t)$ is presented in (4.20) and $\phi_0(t) = \phi^+_{out,0}(t)$ in (4.70).

The approximated wave solution can provide valuable insights into the spatio-temporal behavior of the individuals with respect to the age-structured model. The next section demonstrates how the problem of constructing the wave solution can be reduced to the problem of finding a upper lower solution pair.

4.6 Supplements to the monotone iterative method

In the previous sections we have been mostly dealing with the reduced forms of the wave equation. For instance, it was hypothesized that the immature population does not propagate into the spatial domain and therefore the diffusion of the immature population is set to zero (i.e. $\alpha = \int_0^r D_I(a)da = 0$ where $D_I(a)$ represents the diffusion rate of the immature individuals at age a and r is the maturation time). In this section we are concerned with the case that part or all of the immature population has mobility and the parameter α is not necessarily small. Also there is no restriction on the coefficient D_m corresponding to the spatial variations of the mature population. Then the problem of finding the traveling wave solution is solved by employing a monotone iterative method. This has been done in the work by So et al. [165] and a few other works [103],[191], [192], [197].

In the following we will briefly outline this method, then we will include our supplements to the method which make the method less dependent on the numerics and reduce the overall computational time and efforts. Furthermore, the problem is treated for a general birth function $b(\phi)$ with a few conditions that will be described later.

Define the functional $H : C(\mathbb{R}, \mathbb{R}) \to C(\mathbb{R}, \mathbb{R})$ by,

$$H(\phi)(t) := \epsilon \int_{-\infty}^{\infty} b(\phi(t + y - c\tau)) f_\alpha(y)dy, \ \phi \in C(\mathbb{R}, \mathbb{R}), t \in \mathbb{R}. \tag{4.72}$$

Then the wave equation with the boundary conditions is given by,

$$c\phi^{'}(t) = D_m\phi^{''}(t) - d_m\phi(t) + H(\phi)(t), \tag{4.73}$$

$$\lim_{t\to-\infty} \phi(t) = \phi_1, \lim_{t\to\infty} \phi(t) = \phi_2. \tag{4.74}$$

Definition 9. *A function $\phi \in C(\mathbb{R}, \mathbb{R})$ is called an upper (respectively lower solution) of (4.73) if it is differentiable and it satisfies (4.73) with the sign $\geq$ (respectively $\leq$)*

Define a wave profile set of traveling wave solutions as

$$\Gamma = \left\{ \phi \in C(\mathbb{R}, \mathbb{R}) \middle| \phi(t) \text{ is non-decreasing in } t \in \mathbb{R}, \lim_{t\to\infty} = \phi_2, \lim_{t\to-\infty} = \phi_1 \right\}. \tag{4.75}$$

It can be shown that if $b(\phi)$ is increasing in the interval $[\phi_1, \phi_2]$, then $H(\phi)(t) \geq 0$ for all $t \in \mathbb{R}$, $H(\phi)(t)$ is non-decreasing with respect to $t \in \mathbb{R}$ and also with respect to $\phi \in C(\mathbb{R}, \mathbb{R})$.

Using these properties of $H(\phi)(t)$ and an iterative technique, the problem of constructing a traveling wavefront is reduced to the problem of finding an upper $\overline{\phi}$ and lower $\underline{\phi}$ solutions of (4.73) with the following conditions:

C1) $\overline{\phi} \in \Gamma$

C2) $\phi_1 \leq \underline{\phi}(t) \leq \overline{\phi}(t) \leq \phi_2$ for all $t \in \mathbb{R}$

C3) $\underline{\phi}(t) \neq 0$.

More specifically, under monotonicity condition (i.e. $\phi_1 < \phi_M$, where ϕ_M is the local maximum of $b(\phi)$), the solution of (4.73)-(4.74) is obtained by solving the following equation iteratively,

$$cv_n'(t) = D_m v_n''(t) - d_m v_n(t) + H(v_{n-1})(t), t \in \mathbb{R}, n = 1, 2, \ldots, \tag{4.76}$$

with boundary conditions

$$\lim_{t\to-\infty} v_n(t) = \phi_1 \text{ and } \lim_{t\to\infty} v_n(t) = \phi_2, \tag{4.77}$$

where $v_0(t) = \overline{\phi}(t)$, $t \in \mathbb{R}$.

In other words, $\underline{\phi}(t) \leq v_n(t) \leq v_{n-1} \leq \overline{\phi}(t)$ for all $n = 1, 2, \ldots$ and $\phi(t) = \lim_{n\to\infty} v_n(t)$ is a solution of (4.73)-(4.74). Considering that $H(v_{n-1})(t)$ is a known function of t, equation (4.76) is a non-homogeneous second order linear differential equation that has the following solution,

$$v_n(t) = \frac{1}{D_m(\beta_+ - \beta_-)} \left[\int_{-\infty}^{t} e^{\beta_-(t-s)} H(v_{n-1})(s) ds + \int_{t}^{\infty} e^{\beta_+(t-s)} H(v_{n-1})(s) ds \right], \tag{4.78}$$

where $t \in \mathbb{R}$, $n = 1, 2, \ldots$ and $\beta_{\pm} = \frac{c \pm \sqrt{c^2 + 4D_m d_m}}{2D_m}$. Then it can be shown (see Theorem 4.3 of [165]) that $v_n \in \Gamma$, $\underline{\phi}(t) \leq v_n(t) \leq v_{n-1}(t) \leq \overline{\phi}(t)$. For all $n = 1, 2, \ldots$, each v_n is an upper solution and $\lim_{n \to \infty} v_n(t) = \phi(t)$.
The work by So et al. [165] shows that

$$\overline{\phi}(t) = \min\left\{\phi_2, \phi_2 e^{\lambda_1 t}\right\}, \tag{4.79}$$

and

$$\underline{\phi}(t) = \max\left\{0, \phi_2(1 - Ne^{\delta t})e^{\lambda_1 t}\right\}, \tag{4.80}$$

are a pair of upper and lower solutions when the birth function $b_1(\phi)$ is considered with $q = 1$ and $\frac{\epsilon p}{d_m} < e$, which is for the monotonicity of the wave solution. Here $N > 1$ and $\delta > 0$ are respectively large and small constants and λ_1 is a real positive root of

$$\Delta_c(\lambda) = \epsilon b_i'(0) e^{\alpha\lambda^2 - \lambda c\tau} - (c\lambda + d_m - D_m\lambda^2), \tag{4.81}$$

which is the characteristic equation of the wave equation (4.73).

The study is continued in the work by Liang and Wu [103] where the authors show that the same pair of upper and lower solutions can be used for the birth functions $b_1(\phi)$, $b_2(\phi)$ and $b_3(\phi)$ in a more general form of the model that includes advection. Using Matlab the monotone iterative method is implemented in the present work. Figure 4.10 represents the convergence of the iterative wave approximations to the actual wave solution. From left to right, the wave approximations tend to the actual wave solution. Specifically, after n=15 iterations, the approximated wave solutions $v_n(t)$'s become almost identical. Note that $b(\phi) = b_1(\phi), \tau = .3, \epsilon = 1, \alpha = 1, p = 2.5, d_m = 1, D_m = 1, a = 1, c = 5$ and $M = 40$.

Figure 4.11 represents the numerical wave solutions obtained with the monotone iterative method. The parameter values are mainly the same as those mentioned above. It is interesting to compare these Figures with those presented in [103].

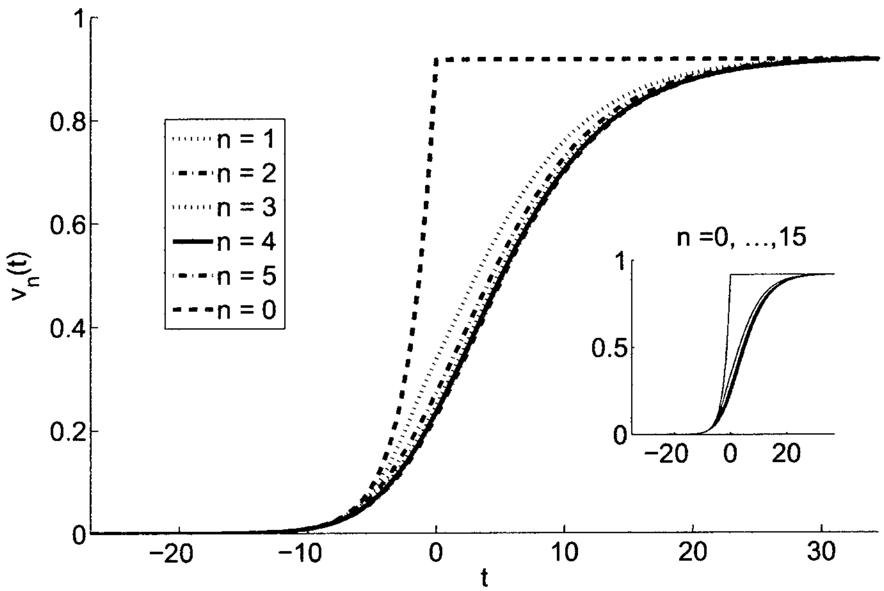


Figure 4.10: A representation for the convergence of the monotone iterative method. After n=15 iterations, $v_n(t)$ approaches to the actual wave solution.

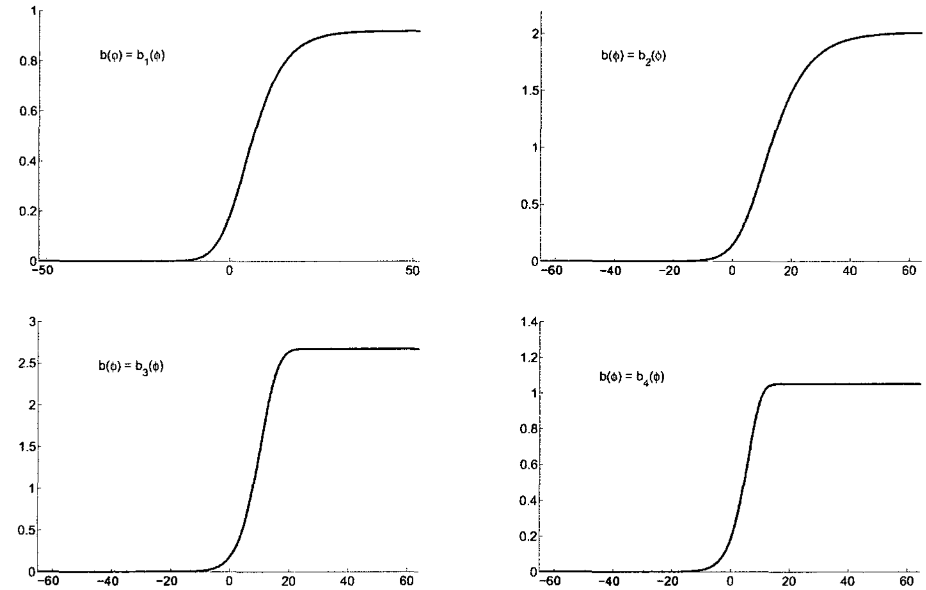


Figure 4.11: Numerical wave solutions obtained with the monotone iterative method.

Note that we need to have the birth functions b_1, b_2 and b_3 satisfy the monotonicity condition. Namely when $b(\phi) = b_1(\phi)$, $\frac{\epsilon p}{d_m} < e^{\frac{1}{q}}$; when $b(\phi) = b_2(\phi)$, $\frac{\epsilon p}{d_m} < \frac{q}{q-1}$ with $q > 1$, and when $b(\phi) = b_3(\phi)$, $\frac{\epsilon p}{d_m} < \frac{1+q}{q}$. Also in all these cases we need $1 < \frac{\epsilon p}{d_m}$ to have two steady states; otherwise, the only steady state of the wave equation in the real domain will be $\phi_1 = 0$.

Some of these conditions can be replaced with less strict conditions. For instance, it has been shown that the iterative methods work under quasi-monotonic or partially quasi-monotonic conditions [75] [74]. Also Schauder's fixed point theorem has been used to prove existence the traveling wavefronts [110] [111]. We will discuss these extensions somewhere else. The main goal of the present section is to provide a supplement to the monotone iterative method. Namely, we would like to obtain approximation of the wave solution through this method. Also, it is our intent to modify the upper and lower solutions in a way that they become independent of the real positive roots of the characteristic equation (4.81). This is important since the method in its present condition is dependent on the numerical computation of λ_1 of (4.81). Before pursuing the above-mentioned goals we would like to comment on some previous works. For this purpose, consider the characteristic equation (4.81). Several studies mention the existence of the unique pair (c^*, λ^*) solution of $\Delta_{c^*}(\lambda^*) = 0$ and $\frac{d\Delta_{c^*}}{d\lambda}(\lambda^*) = 0$. See for example Lemma 4.4 of [165], Lemma 3 of [103] and also Lemma 2.1 of J.Wu [194]. None of these works outline any proof for such a conclusion. Consider the case that $\frac{\tau}{\alpha} = \frac{1}{D_m}$, then from equation (4.81) it can be shown that where c^* must satisfy $\Delta_{c^*}(\lambda^*) = 0$ that is equivalent to

$$\epsilon b_i'(0) e^{\frac{-c^{*2}\tau^2}{4\alpha}} = d_m + \frac{c^{*2}}{4D_m}. \tag{4.82}$$

Equation (4.82) can be solved explicitly. Let

$$z = \frac{c^{*2}\tau^2}{4\alpha} + \frac{\tau^2 d_m D_m}{\alpha}. \tag{4.83}$$

Substituting (4.83) into (4.82) we get

$$\epsilon b_i'(0) e^{\frac{\tau^2 d_m D_m}{\alpha}} e^{-z} = \frac{\alpha}{\tau^2 D_m} z. \tag{4.84}$$

Using the Lambert W function we have

$$z = W\left(\frac{\epsilon\tau^2 D_m b_i'(0)}{\alpha} e^{\frac{\tau^2 d_m D_m}{\alpha}}\right). \tag{4.85}$$

From (4.83) and (4.85) we get that

$$c^* = \left(\frac{4\alpha}{\tau^2} W\left(\frac{\epsilon\tau^2 D_m b_i'(0)}{\alpha} e^{\frac{\tau^2 d_m D_m}{\alpha}}\right) - 4 d_m D_m\right)^{\frac{1}{2}}. \tag{4.86}$$

In the following we discuss the existence of the solution pair (c^*, λ^*) from a general point of view. Define the functions $f(\lambda)$ and $g(\lambda)$ as follows

$$f(\lambda) := \epsilon b'(0) e^{\alpha\lambda^2 - \lambda c\tau}, \tag{4.87}$$

$$g(\lambda) := c\lambda + d_m - D_m\lambda^2. \tag{4.88}$$

Then $g(\lambda)$ has a local maximum at $(\lambda_M, g_M) = \left(\frac{c}{2D_m}, d_m + \frac{c^2}{4D_m}\right)$ and $f(\lambda)$ has a local minimum at $(\lambda_m, f_m) = \left(\frac{c\tau}{2\alpha}, \epsilon b'(0)e^{-\frac{c^2\tau^2}{4\alpha}}\right)$. Note that

$$\Delta_c(\lambda) = f(\lambda) - g(\lambda). \tag{4.89}$$

When $\frac{\tau}{\alpha} = \frac{1}{D_m}$, we have $\lambda^* = \lambda_m = \lambda_M$ and $g_M = f_m$. As shown in the series of equations (4.82)-(4.86), c^* is obtained by solving $g_M = f_m$. Note that since $\lambda^* = \lambda_M = \lambda_m$, the pair (c^*, λ^*) already satisfies $\frac{d\Delta_c^*}{d\lambda}(\lambda^*) = 0$. When $\frac{\tau}{\alpha} \neq \frac{1}{D_m}$, the solution pair (c^*, λ^*) can be numerically found by employing methods such as the Newton's iterative method.

In certain cases (i.e. $\alpha = 0$), we may take advantage of Lambert W function and find the solution. Similar to Section 2.6, λ^* can be expressed as a function of c^*. Nevertheless the expressions are in the implicit forms. Alternatively, it is possible to employ a level curve method to reduce the problem into a logarithmic equation that can be solved numerically. Also in the case that roots λ_1 and λ_2 of (4.81) exist, it is possible to find their upper and lower bounds.

There are algebraic methods to find an upper bound for c^*. For instance, the work by Wu et al. [194] shows $2\sqrt{D_m(\epsilon p - d_m)}$ is an upper bound for c^* when the birth function b_1 is considered and $\frac{\tau}{\alpha} \geq \frac{1}{D_m}$. Following the same procedure it can be shown that for a general birth function when $\frac{\tau}{\alpha} \geq \frac{1}{D_m}$ we have $2\sqrt{D_m(\epsilon b'(0) - d_m)} \geq c^*$ (See the proof of Theorem 2.2 of [194]).

Remark 32. It can be verified that for $\frac{\tau}{\alpha} \geq \frac{1}{D_m}$ and $c > 2\sqrt{D_m(\epsilon b'(0) - d_m)}$ we have $\Delta_c(\lambda_M) < 0$, where $\lambda_M = \frac{c}{2D_m}$ is the maximum of the function $g(\lambda)$ defined in (4.88).

Remark 33. Similar to the Section (iii) from Lemma 4.4 of [165] it can be shown that for $\frac{\tau}{\alpha} \geq \frac{1}{D_m}$ and $c > 2\sqrt{D_m(\epsilon b'(0) - d_m)}$, $\lambda_M = \frac{c}{2D_m} \in (\lambda_1, \lambda_2)$.

The iterative method outlined in previous pages can be improved from different perspectives. Considering the computational aspect of the problem, we would like to reduce the numerical efforts required to find the approximations of the wave solution. Here, the underlying question is whether we can avoid the procedure of root finding. In particular, the root λ_1 of (4.81) is used in the upper solution $\overline{\phi}(t)$ which is the initial estimate of the wave solution. In the following we show that the upper solution $\overline{\phi}(t)$ of the form (4.79) can be modified such that it does not require the root λ_1 of (4.81). Let $\phi_1 = 0$ and consider the following conditions **A1** and **A2**.

A1) b is increasing on the interval $[\phi_1, \phi_2]$ and $\epsilon b^{'}(0) > d_m$.

A2) $b(\phi) < b^{'}(0)\phi$ for $\phi \in [\phi_1, \phi_2]$ and $c > 2\sqrt{D_m(\epsilon b^{'}(0) - d_m)}$.

Define:

$$\overline{\phi}_B(t) := \min\left\{\phi_2, \phi_2 e^{\lambda_B t}\right\}, \tag{4.90}$$

where $\lambda_B \in (\lambda_1, \lambda_2)$. In the following we show that for any $\lambda_B \in (\lambda_1, \lambda_2)$, ϕ_B is an upper solution of the wave equation (4.73).

Lemma 8. Under conditions **A1** and **A2**, $\overline{\phi}_B(t)$ is an upper solution of (4.73).

Proof.

We need to show that $\overline{\phi}_B$ satisfies (4.75) with the equality sign being replaced with $\geq$ almost everywhere. Similar to Lemma 4.5 of [165] we consider two cases: Case (I) : $t \in (0, \infty)$, then $\overline{\phi}_B(t) = \phi_2$, $\phi_B^{'}(t) = \phi_B^{''}(t) = 0$. Since $b(\phi)$ is increasing on $\phi \in [\phi_1, \phi_2]$ we get

$$H(\overline{\phi}_B)(t) - d_m\overline{\phi}_B(t) \leq H(\phi_2)(t) - d_m\phi_2 = 0,$$

which completes the proof for this case.

Case(II) : $t \in (-\infty, 0)$, then $\overline{\phi}_B(t) = \phi_2 e^{\lambda_B t}$, $\overline{\phi}_L^{'}(t) = \phi_2\lambda_B\phi^{\lambda_B t}$. $\overline{\phi}_B^{''}(t) = \phi_2\lambda_B^2\phi^{\lambda_B t}$. By condition **A2** and since $\overline{\phi}_B(t) \leq \phi_2 e^{\lambda_B t}$ for all $t \in \mathbb{R}$ we have

$$\begin{aligned}
&c\overline{\phi}_B^{'}(t) - D_m\overline{\phi}_B^{''}(t) + d_m\overline{\phi}_B(t) - H(\overline{\phi}_B)(t) \\
&\geq \left[c\lambda_B - D_m\lambda_B^2 + d_m\right]\phi_2 e^{\lambda_B t} - \epsilon b^{'}(0)\int_{-\infty}^{\infty}\overline{\phi}_B(t)(t + y - c\tau)f_\alpha(y)dy,
\end{aligned}$$

$$\geq \left[c\lambda_B - D_m\lambda_B^2 + d_m\right]\phi_2 e^{\lambda_B t} - \epsilon b'(0)\phi_2 \int_{-\infty}^{\infty} e^{\lambda_B(t+y-c\tau)} f_\alpha(y)dy,$$
$$= \phi_2 e^{\lambda_B t}\left(c\lambda_B - D_m\lambda_B^2 + d_m - \epsilon b'(0)e^{\alpha\lambda_B^2 - c\tau\lambda_B^2}\right),$$
$$= -\phi_2 e^{\lambda_B t}\Delta_c(\lambda_B) > 0.$$

The last inequality is due to $\Delta_c(\lambda_B) > 0$ for $\lambda_B \in (\lambda_1, \lambda_2)$. See Lemma 3 of [103]. Hence $\overline{\phi}_B(t)$ is an upper solution and the proof is complete. □

Corollary 2. In (4.90) let $\frac{\tau}{\alpha} \geq \frac{1}{D_m}$. If conditions **A1** and **A2** are satisfied then $\overline{\phi}_B(t)$ with $\lambda_B = \frac{c}{2D_m}$ is an upper solution of (4.73).

Proof.

As mentioned in Remark 33, we have $\lambda_M = \lambda_B = \frac{c}{2D_m} \in (\lambda_1, \lambda_2)$. Then using Lemma 8, $\overline{\phi}_B(t)$ is an upper solution. □

Consider the following condition on the birth function $b(\phi)$.

A3) $b(\phi) > \phi(1 - r\phi^s)$, where $r > 0$ and s is the largest odd integer that holds the inequality.

Note that the Lemma 5 of [103] only considers the birth functions b_1, b_2 and b_3 which already satisfy the condition **A3**. Define the lower solution,

$$\underline{\phi}_B(t) = \max\left\{0, \phi_2(1 - Ne^{\delta t})e^{\lambda_B t}\right\}, \tag{4.91}$$

where $\lambda_B \in (\lambda_1, \lambda_2)$, $N > 1$ is sufficiently large and $\delta > 0$ is a small constant such that $\lambda_B + \delta \in (\lambda_1, \lambda_2)$ and $0 < \delta < s\lambda_B$.

Lemma 9. Under conditions **A1** - **A3**, $\underline{\phi}_B(t)$ is a lower solution of (4.73).

Proof.

The proof is similar to that of Lemma 5 of [103]. Let $z = \frac{1}{\delta}\ln\frac{1}{N}$. Then for $t \in (z, \infty)$,

$\underline{\phi}(t) = 0$ and there is nothing to prove. For $(t \in -\infty, z)$, let $\psi(t) = \phi_2(1 - Ne^{\delta t})e^{\lambda_B t}$. Then similar to the proof of Lemma 5 of [103] we can use the condition **A3** to show that,

$$\begin{aligned} H(\underline{\phi})_B(t) \geq\ & \epsilon b'(0)\phi_2 \left(e^{\lambda_B t} e^{\alpha\lambda_B^2 - c\tau\lambda} - Ne^{\alpha(\lambda_B+\delta)^2 - c\tau(\lambda_B+\delta)}\right) - \\ & \epsilon b'(0) r \int_{-\infty}^{\infty} \psi^{st}(t - c\tau + y) f_\alpha(y) dy. \end{aligned} \tag{4.92}$$

Following the same procedure given in [103] and noting that $\Delta_c(\lambda_B + \delta) < 0$, N can be chosen sufficiently large such that,

$$c\underline{\phi}_B'(t) - D_m \underline{\phi}_B(t) + d_m \underline{\phi}_B(t) - H(\underline{\phi}_B)(t) \leq 0.$$

□

Considering the wave profile set Γ defined in (4.75) we can see that $\underline{\phi}_B(t), \overline{\phi}_B(t) \in \Gamma$. Furthermore,

$$\phi_1 \leq \underline{\phi}_B(t) \leq \overline{\phi}_B(t) \leq \phi_2 \text{ and } \underline{\phi}_B(t) \neq 0.$$

Hence all three conditions **C1**, **C2** and **C3** are satisfied and the solution of (4.73)-(4.74) can be iteratively found through the formula (4.76). As mentioned before,the actual iterative method requires an upper solution as the initial guess. A comparison of $\overline{\phi}(t)$ in (4.79) and $\overline{\phi}_B(t)$ in (4.90) indicates that $\phi(t) \geq \overline{\phi}_B(t)$. Noting that the iterative method is monotonic (i.e. $v_0 \geq v_1(t) \geq v_2(t) \geq \ldots$), the initial guess $v_0(t) = \overline{\phi}_B(t)$ is closer to the actual solution $\phi(t) = \lim_{n\to\infty} v_n(t)$. Thus the wave solution is approximated in less amount of time when $\overline{\phi}(t)$ is replaced with $\overline{\phi}_B(t)$. We also note that $\overline{\phi}_B(t)$ is independent of numerical computation of the root λ_1 which reduces the time consumption even more. Figure 4.12 represents such a case. The convergence takes palace after 4 iterations when $\overline{\phi}_B(t)$ is used, while the initial function $\overline{\phi}(t)$ leads a convergence after 15 iterations. Here, the birth function $b(\phi) = b_1(\phi)$ is used. The parameter values used for numerical computations are

$\tau = 3, \epsilon = 1, \alpha = 1, p = 2.5, d_m = 1, D_m = 1, a = .2, c = 4$ and $M = 40$. These values lead to steady states $\phi_1 = 0$ and $\phi_2 = 4.5815$. The values for the other components of the iterative method are $\beta_1 = -0.2361, \beta_2 = 4.2361, \lambda^* = 0.6713, c^* = 2.6258, \lambda_1 = 0.2570, \lambda_2 = 1.6112$ and $\lambda_B = c/2D_m = 2$.

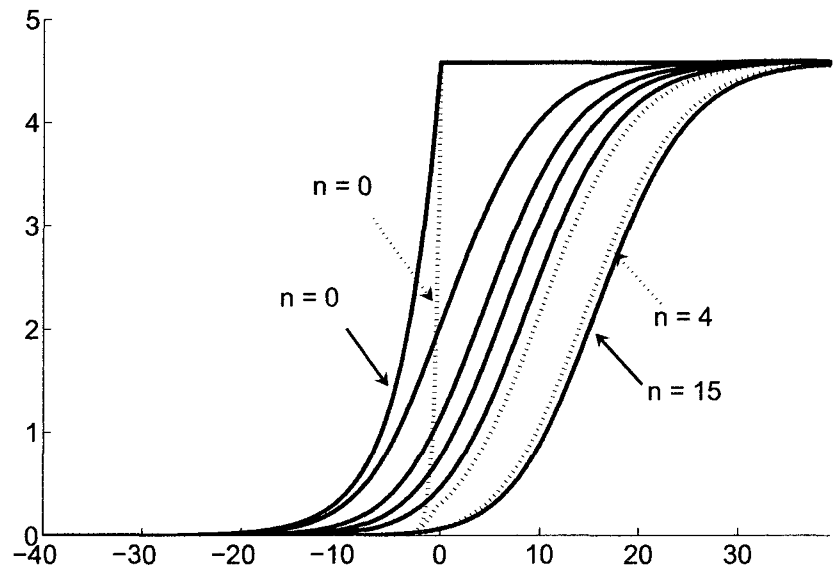


Figure 4.12: The monotone iterative method converges faster (dashed lines) when the initial iteration function $v_0(t) = \overline{\phi}(t)$ is replaced with $v_0(t) = \overline{\phi}_B(t)$. See the text for specific parameter values corresponding to the Figure.

Remark 34. Although the new upper solution $\overline{\phi}_B(t)$ provides a faster convergence and requires less computational efforts. There is a downside in the approach provided here. In particular, the monotonicity of iterative solutions v_n is lost. Also, the price we pay for the faster convergence is less agreement with the theoretical result (1.36) for asymptotic behaviour of ϕ as $t \to -\infty$. In general, the problem is that the definition 9 is not sufficient for monotonicity of the iteration. This has been

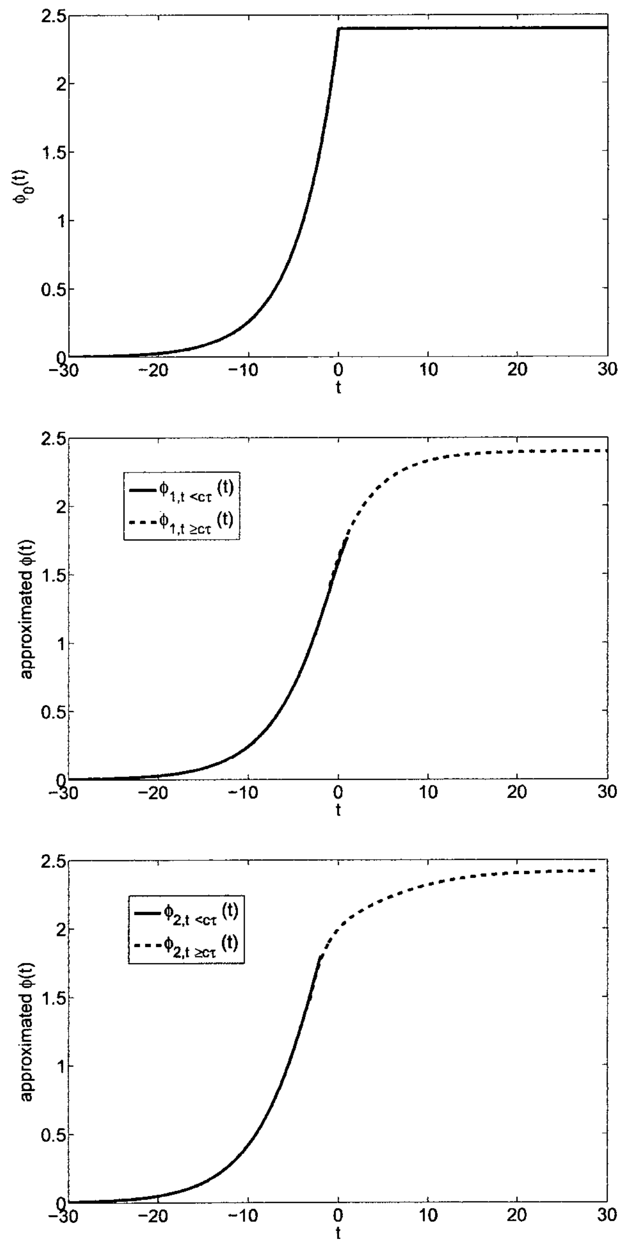


Figure 4.13: The approximated wave solutions with the birth function $b_3(\phi)$. The parameter values are given below. $K_c = 4, \tau = 0.4, c = 4, p = 2.5, \alpha = 1, \epsilon = 1, D_m = 1, d_m = 1$.

reported in the recent work by Wu and Zou [193]. In fact a better way to define the upper and lower solutions is to use (4.78) , by changing the equal sign to $\geq$ and $\leq$ respectively. This has been considered in the recent paper by Wang [182]

In the following we would like to study the iterative formula outlined in (4.78). Specifically, we would like to know what form of solutions are generated with formula (4.78). Hence, we use the symbolic mathematics of the computer package Maple to obtain approximation of the wave solutions. Considering the birth function $b(\phi) = b_3(\phi)$ it can be shown that the wave solution is approximated with series of the form

$$\phi_{approx}(t) = \sum_{k=1}^{n} a_k t^{b_k} e^{c_k t}, \tag{4.93}$$

where a_k, b_k and b_k are constants and $n \geq 1$.
In particular, by setting the parameter values to $K_c = 4, D_m = 1, d_m = 1, \alpha = 1, \epsilon = 1, p = 2.5, \tau = 0.4, c = 4, a = 1, b(\phi) = b_3(\phi)$, we get the following wave approximations for $n = 0, 1$ and 2 respectively.

$$\phi_0(t) = \min\{2.4, 2.4e^{0.22t}\}$$

$$\begin{aligned}
\phi_{1,t\geq c\tau}(t) &= -0.775e^{-0.24t} + 2.4 \\
\phi_{1,t<c\tau}(t) &= 2.27e^{0.22t} - .68e^{0.44t} + 3.65 \times 10^{-6}e^{4.24t}
\end{aligned}$$

$$\begin{aligned}
\phi_{2,t\geq c\tau}(t) &= 2.42 - (0.006 + 0.13t)e^{-0.24t} - 0.53e^{-0.47t} \\
\phi_{2,t<c\tau}(t) &= -2.38e^{0.44t} + 0.71e^{0.67t} + 4.06e^{0.22t} + 3.04 \times 10^{-7}e^{4.68t} - \\
&\quad 0.08e^{0.89t} - 6.82 \times 10^{-13}e^{8.47t} - 1.05e^{4.46t} + (9.51 \times 10^{-7} - 3.44t)e^{4.24t}
\end{aligned}$$

Note that the above approximations are simplified forms of the Maple outputs. The actual the series from Maple outputs are much longer than what is shown here. It can be numerically verified that the approximations are in fairly good agreement with the exact numerical solutions. Figure 4.13 represents the approximated wave solution after 2 iterations. Here, $\phi_1 = 0$ and $\phi_2 = 2.4$ are the steady states of the waves equation. The next section deals with velocity of the traveling wave in the spatial domain.

4.7 Creeping velocity of population expansion: A perturbation method

Existence of traveling wave solutions of the population model (2.7) has been proved in a number of studies. As mentioned before, So et al. [165] proved existence of monotonic traveling wavefronts via iteration method for a specific form of the birth function. Later on the result was extended to two other types of birth functions [103]. The study was continued by considering a general class of nonlocal Reaction-Diffusion equation with small delays which includes the population model (2.7) [139]. Also, there has been progress in finding the minimal wave speed c^* [139] and the lower bound for wave speed c^* [194].

While the main goal of this chapter is to approximate traveling wave solutions, in the present section we extend our work to a different element of the population dynamics. In particular, we would like to study the velocity of the population expansion in the spatial domain for large speeds of wave. The wave equation is obtained from the population model by considering $U(x,t) = \phi(x+ct)$. It is also possible to consider the opposite direction of wave and obtain a slightly different wave equation. Namely, by letting $U(x,t) = \phi(x-ct)$, the wave equation is given by

$$D_m\phi^{''} + c\phi^{'} - d_m\phi + \epsilon\int_{-\infty}^{\infty} b(\phi(t+y+c\tau))f_\alpha(y)dy = 0. \tag{4.94}$$

Considering that the wave solution exists for speeds greater than a critical values c^*, we are concerned with large values of wave speed c. In particular, when $c \gg 0$, the wave equation (4.94) is analogous to a delayed mechanical system with large friction. To be more specific, let D_m be fixed and the ratio $0 < \frac{D_m}{c} \ll 1$. Equation

(4.94) is rewritten as

$$D_m\phi''(t) + c\phi'(t) + g_\phi^\tau(t) = 0, \tag{4.95}$$

where

$$g_\phi^\tau(t) = -d_m\phi(t) + \epsilon\int_{-\infty}^{\infty} b(\phi(t+y+c\tau))f_\alpha(y)dy.$$

Introducing the velocity of wave $v(t) = \phi'(t)$ we may write

$$\frac{dv}{dt} = \frac{c}{D_m}v - \frac{1}{D_m}g_\phi^\tau. \tag{4.96}$$

Equation (4.96) can be written in the differential form

$$\mu(t)dv + \frac{1}{D_m}\mu(t)\left[g_\phi^\tau(t) + cv(t)\right]dt = 0, \tag{4.97}$$

where $\mu(t)$ is a function that makes the left-hand side an exact differential equation. It is interesting to observe that delay function g_ϕ^τ is independent of v and plays no part in determining $\mu(t)$. Then similar to delay-independent first-order differential equations, we chose $\mu(t) = e^{-\frac{c}{D_m}t}$. Hence equation (4.97) is written in the form of

$$d\left[e^{-\frac{c}{D_m}t}v(t)\right] = -\frac{1}{D_m}e^{-\frac{c}{D_m}t}g_\phi^\tau(t)dt. \tag{4.98}$$

Integrating the last equation from 0 to t gives

$$v(t) = e^{-\frac{c}{D_m}t}v(0) - \frac{1}{D_m}\int_0^t e^{-\frac{c}{D_m}(t-s)}g_\phi^\tau(s)ds. \tag{4.99}$$

Using integration by parts, the integral in (4.99) yields

$$\int_0^t e^{-\frac{c}{D_m}(t-s)}g_\phi^\tau(s)ds = \frac{D_m}{c}e^{-\frac{c}{D_m}(t-s)}g_\phi^\tau(s)\Big]_0^t - \frac{D_m}{c}\int_0^t e^{-\frac{c}{D_m}(t-s)}g_\phi'^\tau(s)v(s)ds. \tag{4.100}$$

By repeating the integration by parts it can be seen that the integral term on the right-hand side of (4.100) is of order $O(\frac{1}{c^2})$. Hence, from (4.99) to (4.100) we find that

$$v(t) = e^{-\frac{c}{D_m}t}v(0) - \frac{D_m}{c}g_\phi^\tau(t) + \frac{D_m}{c}e^{-\frac{c}{D_m}t}g_\phi^\tau(0) + O\left(\frac{1}{c^2}\right). \tag{4.101}$$

Since c is very large, the first and the third term on the right-hand side vanish exponentially. Hence the velocity of population expansion in the spatial domain is approximated by

$$\begin{aligned} v(t) &= -\tfrac{D_m}{c} g_\phi^\tau(t) \\ &= -\tfrac{D_m}{c}\left(-d_m\phi(t) + \epsilon\int_{-\infty}^{\infty} b_i(\phi(t+y+c\tau)) f_\alpha(y)dy\right). \end{aligned} \tag{4.102}$$

This is also equivalent to an approximation of the wave equation. Namely,

$$\phi'(t) = -\frac{D_m}{c} g_\phi^\tau(t). \tag{4.103}$$

To solve (4.103) for the case $\alpha = 0$, we may employ the method of steps in a reverse mode. In particular, assuming that $\phi(t) \simeq \phi_2$ for $t \geq M$, where $M > 0$ is fixed and sufficiently large, the approximated wave equation (4.103) can be solved as described below. The DDE problem associated with (4.103) and one of the boundary conditions is given by

$$\begin{cases} \phi'(t) &= -\frac{1}{c}(-d_m\phi(t) + \epsilon b_i(\phi(t+c\tau))), \\ \phi(t) &= \phi_2 - \eta \text{ for } t \geq M, \end{cases} \tag{4.104}$$

This is where $\eta > 0$ is a small constant.

As demonstrated in Section 4.2, the method of steps can be reversely used to obtain the solution $\phi(t)$ for any desired interval, with $n \in \mathbb{Z}^+$. However, we should note that the original wave equation (4.94) is subject to two boundary conditions and there is no guarantee that the above solution matches the approximated condition $\phi(-M) = \phi_1$. Then, similar to Section 4.2, a boundary layer approach can be employed to deal with the fast solution in the boundary layer.

For c large (i.e. $\frac{D_m}{c} \ll 1$), it can be shown that the velocity $v(t)$ of the wave solution $\phi(t)$ dies out quickly. In particular, suppose that $g_\phi^\tau(t)$ is a priori bounded (i.e. there exist $k_1 > 0$ and $k_2 > 0$ such that $|g_\phi^\tau(t)| \leq k_1$ if $|\phi(0)| \leq k_2$) then from equation (4.99) we get that

$$|v(t)| \leq e^{-\frac{c}{D_m}t}|v(0)| + \frac{k_1}{D_m}\int_0^t e^{-\frac{c}{D_m}(t-s)}ds$$

$$\leq e^{-\frac{c}{D_m}t}\,|v(0)| + \frac{k_1}{c}(1 - e^{-\frac{c}{D_m}t}). \tag{4.105}$$

Hence as t increases, there is barely any fluctuation in the solution $\phi(t)$. In other words, the wave loses its initial velocity $v(0)$ very quickly and settles down in a creeping motion. Figure 4.14 represent the velocity of wave with the birth function $b(\phi) = b_1(\phi)$. Here we have used the monotone iterative method to obtain the wave solution; then using the equation (4.99) the velocity is obtained. Note that the increases to the value of speed result in creeping motion of the wave (i.e. the velocity dies out very quickly). From an ecological point of view, when the population is propagating in the spatial domain at a large speed, the propagation does not last very long. In general, creeping velocity in mechanical systems with

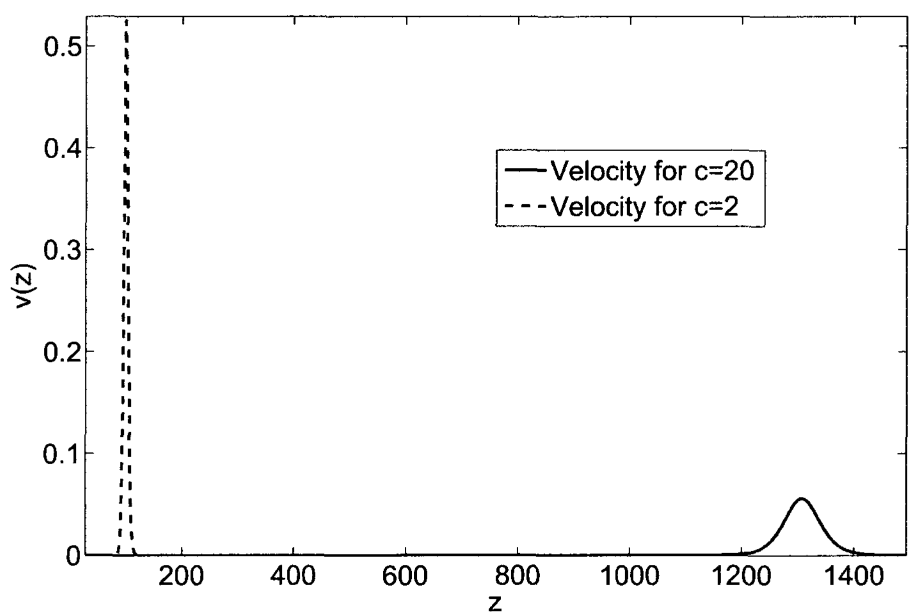


Figure 4.14: Velocity of wave for c=20 and c = 2. Increases to the value of speed result in creeping motion of the wave.

periodic solutions may result in a special feature known as relaxation oscillation. If a system admits a periodic solution, then a drastic change to one of the parameters may turn the periodic solution into a relaxation oscillation. This is described as a periodic behavior in which there are intervals of time with small fluctuations in the solution followed by short intervals of time in which huge changes in solution take place. An example of this can be found in Volterra-Lotka equations,

$$\begin{cases} \dot{x} = ax - bxy, \\ \dot{y} = bxy - cy, \end{cases} \tag{4.106}$$

where $x, y \geq 0$ are prey and predator respectively.
The steady state $(c/b, a/b)$ is a stable center with periodic orbits around it. Considering the birth rate q of prey much smaller than the death rate c of the predator, the periodic solution of (4.106) near the center changes to an oscillatory behavior of x and y with some relations for the predator y [125]

Here, the underlying question is whether large increases to speed c leads to certain fast-slow behavior in the (ϕ, v) phase-plane. For instance, Van der Pol's equation, $\ddot{x} + x = \mu(1 - x^2)\dot{x}$, admits such a behavior when $\mu \gg 1$. Details of the analysis can be found in Chapter 12 of [176]. Here we use a similar methodology. The first step is to transform the wave equation into a delayed Lienard system. Define the transformation $T : \phi, v) \rightarrow (\phi, \psi)$ by

$$\psi = \frac{1}{c}(D_m \phi^{'} + c\phi). \tag{4.107}$$

Then taking the derivative of (4.107) and using (4.95) we get that

$$\begin{aligned} \psi^{'} &= \tfrac{1}{c}(D_m \phi^{''} + c\phi^{'}), \\ &= -\tfrac{1}{c} g_{\phi}^{\tau}(t). \end{aligned} \tag{4.108}$$

Hence the wave equation (4.95) takes the following form of a delayed Lienard planar system,

$$\begin{cases} \phi^{'} = \frac{c}{D_m}(\psi - \phi), \\ \psi^{'} = -\frac{1}{c} g_{\phi}^{\tau}. \end{cases} \tag{4.109}$$

The equation for phase-flow in the (ϕ, ψ)-plane becomes

$$(\psi - \phi)\frac{d\psi}{d\phi} = -\frac{D_m}{c^2} g_\phi^\tau. \tag{4.110}$$

As $c^2 \gg 1$, the right-hand side of (4.110) is very small. Considering this small value as zero, the orbits can be described by either $\psi = \phi$ or ψ =constant. Using (4.107) and solving for ϕ the former case implies that ϕ =constant. While the latter case gives rise to $\phi(t) = e^{-\frac{c}{D_m}t}(k_1 e^{-\frac{ct}{D_m}} + k_2)$, where k_1 and k_2 are constants. This suggests the nonexistence of periodic fast-slow solutions. In fact, small perturbations near the origin will quickly die out and the solution curves return to the steady state $\phi = 0$ after a short period of time.

In summary, the present chapter includes a number of techniques for construction of the traveling wavefronts. These techniques are used according to the nature of the wave equation. When the immature population is immobile (i.e. $\alpha = 0$) and the mature population diffuses slowly (i.e. $0 < D_m \ll 1$), a boundary layer method is used to obtain approximations of the wave solution. When the restriction about the mature spatial expansion is removed an extended differential transform is applicable to the problem. In the case that the immature population diffuses slowly, an asymptotic expansion method is employed to approximate the wave solution. Finally, for the general wave equation with none of the above restrictions, the monotone iterative method is employed to find the wave solution iteratively. This leads to a general form of the approximated wave that can be specified according to the certain birth functions and parameter values. The last section of this chapter shows that when the wave $\phi(t)$ is traveling in the spatial domain with a fast speed, the significant changes in the values of $\phi(t)$ ends quickly .

Chapter 5

Model developments

Mathematical modeling of population dynamics has proven to be useful in discovering the relation between species and their environment. This includes the study and assessment of spatio-temporal changes in population density and estimation of speed of population dispersal. While various continuous and discrete models have been employed for over half a century, recently developed delayed nonlocal Reaction-Diffusion (RD) models have drawn special attention. In the first chapter, we described how mathematical models of population dynamics became sophisticated. Namely, spatially homogeneous models were equipped with discrete or distributed delay; diffusion and advection terms were added to the models and factors such as mature and immature age classes [174] and nonlocality of individuals [29], [30] were considered in the modeling processes.

Previous chapters in this work dealt with a certain class of delayed nonlocal RD model proposed by So et al. [165]. Although the model considers several factors connected to the real world, it is constructed based on a one-dimensional spatial domain. Then the obvious question is whether the model can be developed with respect to a two-dimensional domain. There are a few works devoted to such development. We will discuss these works in the first section of this chapter. In Section

5.2 we present our model development with respect to symmetric two-dimensional bounded domains. Finally, in Section 5.3, we demonstrate how under some conditions, the two-dimensional model may be reduced to simpler forms.

5.1 Overview of recent developments

Let $u(t, a, x, y)$ denote the density of the population of the species at time $t > 0$, the age $a \geq 0$ and the spatial position $(x, y) \in \Omega \subseteq \mathbb{R}^2$. Dynamics of single species age-structured populations can be represented [113] by the following equation,

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} = D(a)\left(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2}\right) - d(a)u, \tag{5.1}$$

where $D(a)$ and $d(a)$ are respectively diffusion and death rates at age a. Equation (5.1) describes basic space-time dynamics of population of a single species with respect to age a. When there is no age dependence (i.e. when $\frac{\partial u}{\partial a} = 0$, $D(a) = D$ and $d(a) = d$ with $D, d > 0$), equation (5.1) becomes a linear RD equation that can be directly solved with the method of separation of variables. Let $\tau \geq 0$ be the maturation time for the species. Then the total matured population at time t and position (x, y) is given by,

$$w(t, x, y) = \int_{\tau}^{\infty} u(t, a, x, y)da. \tag{5.2}$$

Integrating both sides of (5.1) from τ to ∞, using the assumption $u(t, \infty, x, y) = 0$, equating the reproduction density with birth function of mature population (i.e. $u(t, 0, x, y)) = b(w(t, x, y)))$ and considering the diffusion and death rates to be age independent (i.e. $D(a) = D_m$ and $d(a) = d_m$ for $a \in [\tau, \infty)$ with D_m, $d_m > 0$) we get

$$\frac{\partial w}{\partial t} = u(t, \tau, x, y) + D_m\left(\frac{\partial^2 w}{\partial x^2} + \frac{\partial^2 w}{\partial y^2}\right) - d_m w. \tag{5.3}$$

Using a procedure outlined in [165], [104], [186], $u(t,\tau,x,y)$ can be replaced with an integral term which represents the nonlocality of individuals. In other words, the integral term in the model is a weighted spatial averaging over the entire domain, which justifies the fact that individuals may have been anywhere in the spatial domain at previous times. (See Chapter 1 for more details).

The form of the integral term depends on the shape of the spatial domain, boundedness and unboundedness, dimension of the domain and the boundary conditions. As described in [165], when the spatial domain is one-dimensional and unbounded, the population model is given as equation (2.7), that is,

$$\frac{\partial w}{\partial t} = D_m \frac{\partial^2 w}{\partial x^2} - d_m w + \epsilon \int_{-\infty}^{\infty} b(w(t-\tau, y)) f_\alpha(x-y) dy. \tag{5.4}$$

The traveling wavefront of (5.4) has been constructed in [165] with the birth function $b_1(w)$. Later Liang and Wu [103] developed the model by adding the advection term $B_m \frac{\partial w}{\partial x}$ to the right-hand side of (5.4). They studied the traveling wavefronts with the birth functions $b_1(w)$, $b_2(w)$ and $b_3(w)$. Their work includes numerical approximation of traveling wavefronts and formation of single and multi-hump wave solutions when the monotonicity condition is violated. There are also other models similar to equation (5.4). For instance Al-Omari and Gourley [8] generalized the work by Aiello and Freedman [4] and derived the following model:

$$\frac{\partial w}{\partial t} = D_m \frac{\partial^2 w}{\partial x^2} - d_m w + \epsilon \int_0^{\tau} G(x,y,s) f(s) e^{-\gamma s} b(w(y, t-s)) dy ds, \tag{5.5}$$

where $\Omega \subset \mathbb{R}$ is a bounded domain, f is a probability function satisfying $\int_0^\tau f(s)ds = 1$ and G is a kernel derived from solving the heat equation and satisfies $\int_\Omega G(x,y,t)dx = \int_\Omega G(x,y,t)dy = 1$. The work by Ou and Wu [139] considers the general equation (1.91) in a one-dimensional domain which embodies a large number of models including (5.4). They show that for $\tau > 0$ small, the traveling wavefront exists if it exists when $\tau = 0$. A few other works (e.g. [181]) include advection and lift the constraint $\tau \geq 0$ being sufficiently small. Nevertheless, due to the fact that the form of the function f in (5.5) is not specified, the outcomes remain at the level of existence and uniqueness and the actual traveling wave solution is not constructed. Regarding the model developments, there are two studies that take advantage of the above procedure and derive models with respect to two-dimensional spatial domains. The first work is by Liang et al. [104] which considers the population growth of a single species living in two-dimensional bounded domain. Namely the model is developed by considering $\Omega \subset \mathbb{R}^2$ as the rectangle $[0, L_x] \times [0, L_y]$ and zero flux boundary conditions for $u(t, \tau, x, y)$ in time frames $t \in [s, s+\tau]$. Finding $u(t, \tau, x, y)$, equation (5.3) is changed to

$$\frac{\partial w}{\partial t} = F(w(t-\tau, \cdot), x, y) + D_m \left(\frac{\partial^2 w}{\partial x^2} + \frac{\partial^2 w}{\partial y^2}\right) - d_m w. \tag{5.6}$$

The function F is given by

$$\begin{aligned} F(x, y, w(t-r, \cdot)) \;\; = \;\; & \tfrac{\epsilon}{L_x L_y} \textstyle\int_0^{L_x} \int_0^{L_y} b(w(t-r, z_x, z_y)). \\ & \{\, 1 + \textstyle\sum_{n=1}^{\infty} \left[\cos \frac{n\pi(x-z_x)}{L_x} + \cos \frac{n\pi(x+z_x)}{L_x}\right] e^{-\alpha(\frac{n\pi}{L_x})^2} \\ & + \textstyle\sum_{m=1}^{\infty} \left[\cos \frac{m\pi(y-z_y)}{L_y} + \cos \frac{m\pi(y+z_y)}{L_y}\right] e^{-\alpha(\frac{m\pi}{L_y})^2} \\ & + \textstyle\sum_{n=1}^{\infty} \sum_{m=1}^{\infty} \left[\cos \frac{n\pi(x-z_x)}{L_x} + \cos \frac{n\pi(x+z_x)}{L_x}\right] . \\ & \left[\cos \frac{m\pi(y-z_y)}{L_y} + \cos \frac{m\pi(y+z_y)}{L_y}\right] . \\ & e^{-\alpha[(\frac{n\pi}{L_x})^2 + (\frac{m\pi}{L_y})^2]} \,\} \, dz_x dz_y. \end{aligned} \tag{5.7}$$

In the same way, the work by Liang et al. continues to derive models with respect to zero Dirichlet or zero mixed boundary conditions (see [104]) for more details). With the birth functions $b_1(w)$ and $b_2(w)$, they study the numerical solutions of the model, where asymptotically stable steady states and periodic wave solutions are observed.

The second work on model derivation for two-dimensional spatial domain is due to Weng et al. [186]. The major difference with the first work is that the domain is unbounded on two sides of the rectangle. In other words, $\Omega \subset \mathbb{R}^2$ is a strip in the form of $\Omega = (-\infty, \infty) \times [0, L]$ with $L > 0$. Then following the same procedure as outlined in [104] we get the equation (5.6) with function F given by

$$F(w(t-\tau,\cdot),x,y)=\int_{\mathbb{R}}\int_0^L \Gamma(\alpha,x,z_x,y,z_y)b(w(t-\tau,z_x,z_y))dz_xdz_y, \tag{5.8}$$

where $\Gamma(t,x,z_x,y,z_y)=\Gamma_1(t,x,z_x)\Gamma_2(t,y,z_y)$, $\Gamma_2=\frac{1}{\sqrt{4\pi t}}e^{-\frac{(y-z_y)^2}{4t}}$ and $\Gamma_1(t,x,z_x)$ is the Green's function of the boundary value problem,

$$\begin{cases} \frac{\partial W}{\partial t}=0 & t>0, x\in(0,L), \\ BW(t,x)=0 & t\geq 0, x=0,L. \end{cases} \tag{5.9}$$

Here $BW(t,x)$ denotes zero flux or zero mixed boundary conditions.
Using the theory of asymptotic speed of spread and monotone traveling waves, the nonexistence of traveling waves with wave speed $0<c<c^*$ and existence result when $c\geq c^*$ are established in [186], where c^* is the minimal speed.

In the next section we will develop a delayed nonlocal RD model in two-dimensional bounded domains with symmetry.

5.2 A nonlocal RD model in symmetrical domain

As briefly discussed in the previous section, the spatial domain has a great impact in the final form of the derived model. While considering a two-dimensional spatial domain in process model derivation seems to be more realistic, the shape of the spatial domain and the applicable boundary conditions are also important factors that must be carefully dealt with. The work by Weng et al. [186] considers an unbounded strip spatial domain $(0,L)\times\mathbb{R}\subset\mathbb{R}^2$. Nevertheless their work does not offer any justification for the chosen domain and the boundary conditions. Instead, the work emphasizes the mathematical aspects of the model and the authors state that the spatial domain in the form of a strip allows the possibility to "discuss two very important asymptotic properties (i.e. traveling waves and spread speed) of the population model as $t = \infty$" (see page 3932 of [186]).

We believe, similar to the one-dimensional unbounded domain, considering an unbounded strip may tie with the Smith-Thieme approach (see Chapter 1). Namely, the work by So et al. [166] demonstrates how the lattice delay differential model (1.82), population distributed in a line of infinitely many patches (i.e. sub-habitants of an environment) can be extended to the continuous model (5.4) with delay and nonlocality. On the other hand, the work by Weng et al. [186] considers four zero valued Neumann or mixed boundary conditions that are limited according to the behavior of individuals on the boundaries $x = 0$ and $x = L$. Similarly, the work by Liang et al. [104] does not offer any explanation on the chosen shape of the bounded domain (i.e. rectangle) and the boundary conditions resulting in various forms of the model. Certainly a mathematical model would be more compelling if it were justified according to the theoretical aspect of the population dynamics.

The importance of the following model development comes from the fact that we have endeavored to justify the choice of the spatial domain and the corresponding boundary conditions. We argue that a bounded two-dimensional disk might be a suitable choice of spatial domain for dispersal of certain single species. In particular, there are a number of studies simulating natural environments by placing the immature population at the center of two-dimensional disks and observing the spread of population over time. For instance, Gomes and Zuben [56] employed a circular arena for radial dispersion of larvae of the blowfly *Chrysomya albiceps*. It is known that after exhaustion of food sources, larvae begin spreading in search of additional food sources. Then the natural environment can be simulated under experimental conditions by employing circular arenas with sufficiently large diameters (i.e. 50 cm).

Also, Roux et al. [148] investigated the behavior of the larval dispersal of *Calliphoridae* flies prior to pupation. The study includes statistical results of the shape of the larval dispersal in southwest France in outdoor experimental conditions. The authors found that the shape of the dispersal is circular and has a concentric distribution around the feeding zone. Moreover, the study confirms that there was no preferential direction taken by larvae, hence the choice of diffusion term in the model seems to be reasonable. Although these studies are conducted for dispersal of the larval population, the use of a circular domain and circular dispersal of larvae give us enough motivation to develop the delayed nonlocal model with respect to circular domains. Morphological aspects of the larval *Chrysomya albiceps* were investigated in a number of studies (see for example [34]). In particular, there are three stages (i.e. instars) during the larval development of *Chrysomya albiceps* flies. The cephalopharyngeal skeleton of larva develops during the instars. The full development of the skeleton takes place in the third instar. Therefore, in our study the third instar is considered as the age structure of the larval population. In addition, larva displacement takes place always in the landscape and individuals cannot fly. Thus it is reasonable to consider a two rather than three-dimensional spatial domain. On the other hand we show that the choice of circular domain can bring valuable insights into the study of symmetric spatial dispersal of individuals.

Following the same procedure outlined in Section 5.1, dynamics of the single species population can be described with equation (5.3), where the spatial domain $\Omega \subset \mathbb{R}^2$ is considered as a two-dimensional disk centered at origin with radius $R > 0$. Since the domain Ω is a disk it is suitable to rewrite (5.3) in polar coordinates. Then we have,

$$\frac{\partial w}{\partial t} = u(t, \tau, r, \theta) + D_m \left(\frac{\partial^2 w}{\partial r^2} + \frac{1}{r}\frac{\partial w}{\partial r} + \frac{1}{r^2}\frac{\partial^2 w}{\partial \theta^2} \right) - d_m w. \tag{5.10}$$

Similar to [165], [104], [186], we need to eliminate $u(t, \tau, r, \theta)$ in order to obtain an equation for $w(t, x, y)$. For $s \geq 0$ fixed, define

$$V^s(t, r, \theta) = u(t, t-s, r, \theta) \text{ with } s < t \leq s + \tau.$$

Then considering (5.1) in polar coordinates, it follows that for $s \leq t \leq s+\tau$,

$$\begin{aligned} \frac{\partial V^s}{\partial t}(t,r,\theta) &= \frac{\partial u}{\partial t}(t,a,r,\theta)\,|_{a=t-s} + \frac{\partial u}{\partial a}(t,a,r,\theta)\big|_{a=t-s}, \\ &= D(t-s)\left(\frac{\partial^2 V^s}{\partial r^2} + \frac{1}{r}\frac{\partial V^s}{\partial r} + \frac{1}{r^2}\frac{\partial^2 V^s}{\partial \theta^2}\right) - d(t-s)V^s. \end{aligned} \tag{5.11}$$

But note that (5.11) is a linear RD equation that can be solved using the method of separation of variables. Moreover, in the case that the domain is unbounded, the standard theory of Fourier transforms can be used to obtain the general solution of (5.11) (see [165], [104] for more details). Since $u(t,0,r,\theta) = b(w(t,r,\theta))$, we have

$$V^s(s,r,\theta) = b(w(s,r,\theta)). \tag{5.12}$$

The zero Dirichlet boundary condition represents the case in which the region outside the domain is uninhabitable. In other words, individuals die once they diffuse out of the domain (see for example [87]). This makes sense when for instance, individuals are insects on an island. Nevertheless, zero Dirichlet boundary conditions are not suitable in all cases. The book by Kot (see page 289, [87]) considers such conditions as an extremely crude way of capturing spatial heterogeneity. Instead, Gurney and Nisbet's approach is outlined in [65] considers that the spatial domain is unbounded and intrinsic rate of growth decreases with the square of the distance from the center of the range (i.e. a Schrodinger equation).

The zero-flux boundary condition is another approach that takes away the in and out privileges of individuals. Namely, individuals never cross their boundaries. This has been used in several studies (see for example [125], [126] and [87]). Combining the zero-flux and Dirichlet boundary conditions, we get mixed boundary conditions where the flux at each boundary is proportional to the density at the boundary. Hence, the above-mentioned boundary conditions are in fact limiting case of zero mixed boundary conditions. In the following we treat the problem with all three cases mentioned above. Considering zero Dirichlet boundary condition and initial condition described in (5.12), we have

$$\frac{\partial^2 V^s}{\partial t} = D(t-s)\left(\frac{\partial^2 V^s}{\partial r^2} + \frac{1}{r}\frac{\partial V^s}{\partial r} + \frac{1}{r^2}\frac{\partial^2 V^s}{\partial \theta^2}\right) - d(t-s)V^s, \tag{5.13}$$

$$V^s(R, \theta, t) = 0, \tag{5.14}$$

$$V^s(s, r, \theta) = b(w(s, r, \theta)). \tag{5.15}$$

The initial boundary value problem (5.13)-(5.15) can be solved with the method of separation of variables. Let $V^s(r, \theta, t) = h(r, \theta, s)T(t)$; substituting this into (5.13) and separating terms with h from terms with T we find two ordinary differential equations:

$$\frac{T' + d(t-s)T}{D(t-s)T} = \lambda, \tag{5.16}$$

$$h_{rr} + \frac{1}{r}h_r + \frac{1}{r^2}h_{\theta\theta} = \lambda h, \tag{5.17}$$

where λ is the separation constant and $(')$ denotes the derivation of T with respect to t; h_{rr}, h_r and $h_{\theta\theta}$ are the partial derivatives with respect to indices r or θ.
By letting $\lambda = -k^2$ and solving (5.16) we get to

$$T(t) = \exp\left(-\int_s^t (k^2 D(t-\sigma) + d(t-\sigma))d\sigma\right). \tag{5.18}$$

By letting $h(r, \theta) = \rho(r)\Phi(\theta)$ and separation of ρ and Φ in (5.17), we get that the angular part must satisfy

$$\Phi_n'' = -n^2\Phi_n, \tag{5.19}$$

which has the solution

$$\Phi_n(\theta) = A_n \cos n\theta + B_n \sin n\theta, \tag{5.20}$$

where n is an integer.

The radial equation is

$$r^2\rho_n'' + r\rho_n' + (k^2r^2 - n^2)\rho_n = 0, \tag{5.21}$$

which is the well-studied parametric Bessel equation with solution

$$\rho_n(r) = C_n J_n(kr) + D_n N_n(kr), \tag{5.22}$$

where $J_n(kr)$ and $N_n(kr)$ are respectively Bessel and Neumann functions of order n and C_n and D_n are constants. Since $N_n(kr)$ goes to $-\infty$ as $r \to 0$ and we are interested in finite solutions, then we must set $D_n = 0$. Thus $h(r,\theta)$ can be written as a linear combination of $h_n(r,\theta)$ with

$$h_n(r,\theta) = J_n(kr)(A_n \cos n\theta + B_n \sin n\theta). \tag{5.23}$$

In order to satisfy the boundary condition (5.14) we must have $h(R,\theta) = 0$. This means that k cannot be an arbitrary constant and must satisfy

$$J_n(kR) = 0. \tag{5.24}$$

Let $k_{nj}R$ be the $j'th$ zero of $n'th$ order Bessel function $J_n(x)$, the k must be equal to one of the k_{nj}s. The same k_{nj} must be used in (5.16). Hence k^2 in (5.18) is changed to k_{nj}^2 and the general solution of (5.13)-(5.15) is a linear combination of all these terms and is given by

$$V^s(R,\theta,t) = \sum_{n=0}^{\infty}\sum_{j=1}^{\infty} J_n(k_{nj}r)(a_{nj}\cos n\theta + b_{nj}\sin n\theta)\exp\left(-\int_s^t k_{nj}^2 D(t-\sigma) + d(t-\sigma)d\sigma\right), \tag{5.25}$$

where the coefficients a_{nj} and b_{nj} can be determined with the initial condition (5.15). Let D_1 and d_1 denote respectively, the diffusion and death rates of the immature population. Define ϵ and α,

$$\epsilon := \exp\left(-\int_0^{\tau} d_I(a)da\right), \tag{5.26}$$

$$\alpha := \int_0^\tau D_I(a)da. \tag{5.27}$$

Note that equation (5.18) can be rewritten as

$$T(t) = \exp\left(-\int_0^{t-s} (k^2 D(\gamma) + d(\gamma))d\gamma\right). \tag{5.28}$$

When $s = t - \tau$, substituting (5.26)-(5.28) into (5.25) we have

$$V^{t-\tau}(R, \theta, t) = \epsilon \sum_{n=0}^{\infty} \sum_{j=1}^{\infty} J_n(k_{nj} r)(a_{nj} \cos n\theta + b_{nj} \sin n\theta) \exp(-k_{nj}^2 \alpha). \tag{5.29}$$

Define:

$$F_n(r) = \sum_{j=1}^{\infty} a_{nj} J(k_{nj} r), \tag{5.30}$$

$$G_n(r) = \sum_{j=1}^{\infty} b_{nj} J_n(k_{nj} r). \tag{5.31}$$

Then for $s = t - \tau$, using (5.15) we have

$$\sum_{n=0}^{\infty} F_n(r) \cos n\theta + G_n(r) \sin n\theta = b(w(r, \theta, t - \tau)). \tag{5.32}$$

Regarding the parameter r, (5.32) is in the form of Fourier series and therefore $F_n(r)$ and $G_n(r)$ are given by,

$$F_n(r) = \frac{1}{\pi} \int_0^{2\pi} b(w(r, \theta, t - \tau)) \cos n\theta d\theta, \ n = 1, 2, \ldots, \tag{5.33}$$

$$F_0(r) = \frac{1}{2\pi} \int_0^{2\pi} b(w(r, \theta, t - \tau)) d\theta, \ n = 0, \tag{5.34}$$

$$G_n(r) = \frac{1}{2\pi} \int_0^{2\pi} b(w(r, \theta, t - \tau)) \sin n\theta d\theta, \ n = 1, 2, \ldots. \tag{5.35}$$

Substituting (5.33) and (5.34) into (5.30), we have

$$\sum_{j=1}^{\infty} a_{nj} J_n(k_{nj} r) = \frac{1}{\pi} \int_0^{2\pi} b(w(r, \theta, t - \tau)) \cos n\theta d\theta, \ n = 1, 2, \ldots, \tag{5.36}$$

$$\sum_{j=1}^{\infty} a_{nj} J_n(k_{nj} r) = \frac{1}{2\pi} \int_0^{2\pi} b(w(r,\theta,t-\tau)) d\theta, \;\; n = 0. \tag{5.37}$$

Similarly, substituting (5.35) into (5.31), we get

$$\sum_{j=1}^{\infty} b_{nj} J_n(k_{nj} r) = \frac{1}{\pi} \int_0^{2\pi} b(w(r,\theta,t-\tau)) \sin n\theta d\theta, \;\; n = 1, 2, \ldots. \tag{5.38}$$

For n fixed, each of the series (5.36)-(5.38), is recognized as Fourier-Bessel series. To find the coefficients a_{nj} and b_{nj}, we need to multiply both sides by $r J_n(k_{ni} r)$ and integrate from zero to R. Thus, from equation (5.36), we have

$$\int_0^R r J_n(k_{ni} r) \sum_{j=1}^{\infty} a_{nj} J_n(k_{nj} r) dr = \int_0^R r J_n(k_{ni} r) \frac{1}{\pi} \int_0^{2\pi} b(w(r,\theta,t-\tau)) \cos n\theta d\theta, \tag{5.39}$$

with $n = 1, 2, \ldots$.

But note that the Bessel functions are orthogonal with respect to weight function r, i.e.,

$$\int_0^R r J_n(k_{ni} r) J_n(k_{nj} r) dr = 0 \text{ if } k_{ni} \neq k_{nj}. \tag{5.40}$$

Thus, all terms on the left-hand side of (5.39) are zero except the term with $i = j$. We get that

$$a_{ni} \int_0^R r J_n^2(k_{ni} r) dr = \frac{1}{\pi} \int_0^R \int_0^{2\pi} r J_n(k_{ni} r) b(w(r,\theta,t-\tau)) \cos n\theta d\theta dr. \tag{5.41}$$

From properties of the Bessel function we have that

$$\int_0^R r J_n^2(k_{ni} r) dr = \frac{1}{2} r^2 J_{n+1}^2(k_{ni} R). \tag{5.42}$$

Therefore,

$$a_{ni} = \frac{2}{\pi R^2 J_{n+1}^2(k_{ni} R)} \int_0^R \int_0^{2\pi} r J_n(k_{ni} r) b(w(r,\theta,t-\tau)) \cos n\theta d\theta dr, n = 1, 2, \ldots. \tag{5.43}$$

Similarly, applying the same steps to (5.37) and (5.38), we get that

$$a_{0i} = \frac{2}{2\pi R^2 J_1^2(k_{0i} R)} \int_0^R \int_0^{2\pi} r J_0(k_{0i} r) b(w(r,\theta,t-\tau)) d\theta dr, \tag{5.44}$$

$$b_{ni} = \frac{2}{\pi R^2 J_{n+1}^2(k_{ni}R)} \int_0^R \int_0^{2\pi} r J_n(k_{ni}r) b(w(r,\theta,t-\tau)) \sin n\theta d\theta dr, \;\; n = 0,1,2,\ldots. \tag{5.45}$$

Hence all required elements of the model are determined.

Considering that $u(t,\tau,r,\theta) = V^{t-\tau}(t,r,\theta)$, from (5.29) and (5.10) we obtain the following delayed nonlocal RD model with initial history function w_0 and zero Dirichlet boundary condition as follows

$$\begin{aligned} \frac{\partial w}{\partial t} &= D_m \left(\frac{\partial^2 w}{\partial r^2} + \frac{1}{r}\frac{\partial w}{\partial r} + \frac{1}{r^2}\frac{\partial^2 w}{\partial \theta^2} \right) - d_m w + \\ &\epsilon \sum_{n=0}^{\infty} \sum_{i=1}^{\infty} J_n(k_{ni}r)(a_{ni}(w(r,\theta,t-\tau)) \cos n\theta + b_{ni}(w(r,\theta,t-\tau)) \sin n\theta) e^{-k_{ni}^2 \alpha}, \end{aligned} \tag{5.46}$$

$$w(t,r,\theta) = w_0(t,r,\theta) \text{ for } (r,\theta) \in \Omega, \;\; t \in [-\tau, 0] \text{ and} \tag{5.47}$$

$$w(R,\theta,t) = 0. \tag{5.48}$$

where $a_{ni}(w(r,\theta,t-\tau))$ and $b_{ni}(w(r,\theta,t-\tau))$ are given in (5.43)-(5.45) and α is defined in (5.27).

Following the same procedure, we may consider the problem with zero-flux boundary condition and derive a model similar to (5.46). In particular, in problem (5.13)-(5.15), condition (5.14) must be replaced with

$$\frac{\partial V^s}{\partial r}(R,\theta,t) = 0. \tag{5.49}$$

Consequently, (5.24) is replaced with

$$\frac{dJ_n(kR)}{dr} = 0. \tag{5.50}$$

Then $k_{nj}R$ is the $j'th$ zero of nth order of derivative of the Bessel function (i.e. $\frac{dJ_n(x)}{dx}$) and k must be equal to k_{nj}.

Again, the set of eigenfunctions $\{J_n(k_{nj}r)\}$ form a complete set and they are orthogonal to each other with respect to weight function. Hence the only difference in the model is that in expression (5.43)-(5.45), the $\{K_{ni}\}$ is the set of eigenvalues corresponding to the zero-flux boundary condition (5.49). Similarly, a model with nonlocality and delay can be derived with respect to zero mixed boundary condition

$$A\frac{\partial V^s}{\partial r}(R,\theta,t) + BV^s(R,\theta,t) = 0, \tag{5.51}$$

where A and B are constants.

While the model (5.46) can be numerically solved and existence of traveling wave solutions can be investigated, it is a highly nontrivial problem to find approximations of the solutions. On the other hand, the model (5.46) takes into account the angular dependence of w. This means that the population concentrated at origin may have spatial preference in its displacement for the search for food or other necessities. However, this is not the case for some species. As described before, Roux et al. [148], for instance, found that there is no preferred direction in spatial movement of the blowfly larvae. Hence we may consider radial symmetry and other possibilities that reduce the model to a simpler form. These are discussed in the following section.

5.3 Model reductions: radial symmetry, effect of initial heterogeneity

In the following we assume that population dispersion takes place with radial symmetry and there is no preference at any direction. Then the IBVP (5.13)-(5.15) is reduced to

$$\frac{\partial V^s}{\partial t} = D(t-s)\left(\frac{\partial^2 V^s}{\partial r^2} + \frac{1}{r}\frac{\partial V^s}{\partial r}\right) - d(t-s)V^s, \tag{5.52}$$

$$V^s(R,t) = 0, \tag{5.53}$$

$$V^s(r,s) = b(w(r,s)). \tag{5.54}$$

The boundary condition (5.53) is equivalent to the assumption that the habitat is inhospitable beyond $r = R$. The substitution

$$V^s(r,t) = T(t)h(r), \tag{5.55}$$

reduces equation (5.52) to equation (5.16) and

$$h_{rr} + \frac{1}{r}h_r = \lambda h, \tag{5.56}$$

which is a reduced form of equation (5.17).
Let $\lambda = -k^2$; then (5.56) is rewritten as

$$r^2 h_{rr} + r h_r + r^2 k^2 h = 0. \tag{5.57}$$

But this is the parametric Bessel equation (5.21) with $n = 0$. The solution is given by

$$h(r) = C_0 J_0(kr) + D_0 N_0(kr), \tag{5.58}$$

where J_0 and N_0 are respectively Bessel and Neumann functions of order zero. C_0 and D_0 are constants. As indicated before, the Neumann function blows up as $r \to 0$. In fact,

$$N_0(r) \sim \frac{2}{\pi}\ln(\frac{r}{2}) \text{ as } r \to 0. \tag{5.59}$$

Hence we let $D_0 = 0$. It can be shown that

$$J_0(r) = \sum_{q=0}^{\infty} \frac{(-1)^q}{(q!)^2}\left(\frac{r}{2}\right)^{2q}. \tag{5.60}$$

Thus,

$$h(r) = C_0 \sum_{q=0}^{\infty} \frac{(-1)^q}{(q!)^2}\left(\frac{kr}{2}\right)^{2q}. \tag{5.61}$$

In order to satisfy the boundary condition (5.53), we must have $h(R) = 0$, then similar to (5.24) we must have

$$J_0(kR) = 0. \tag{5.62}$$

Let k_jR be the j'th zero of the Bessel function of order zero; then k must be equal to one of k_js. From (5.18), (5.58) and (5.55) we have the solution

$$V^s(r,t) = \sum_{j=1}^{\infty} c_j J_0(k_j r) \exp\left(-\int_s^t k^2 D(t-\sigma) + d(t-\sigma) d\sigma\right). \tag{5.63}$$

Set $s = t - \tau$; using (5.26)-(5.28) we get to

$$V^{t-\tau}(r,t) = \epsilon \sum_{j=1}^{\infty} c_j J_0(k_j r) \exp(-k_j^2 \alpha). \tag{5.64}$$

The constant α is defined in (5.27) and the coefficients c_j are determined by the initial condition (5.54). Namely,

$$b(w(r,t-\tau)) = V^{t-\tau}(r,t). \tag{5.65}$$

Using the fact that (5.64) represents a Fourier-Bessel series, by orthogonality of the Bessel functions and (5.42) we get that,

$$c_j = \frac{2}{R^2 J_1^2(k_j R)} \int_0^R r J_0(k_j r) b(w(r,t-\tau)) dr, \; j = 1, 2, \ldots. \tag{5.66}$$

Hence, the population model of individuals with no directional preference in their spatial dispersion is given by

$$\frac{\partial w}{\partial t} = D_m \left(\frac{\partial^2 w}{\partial r^2} + \frac{1}{r}\frac{\partial w}{\partial r}\right) - d_m w + \epsilon \sum_{j=1}^{\infty} c_j(w(r,t-\tau)) J_0(k_j r) \exp(-k_j^2 \alpha), \tag{5.67}$$

with $0 \leq r \leq R$, $t \geq 0$.

$$w(r,t) = w_0(r,t), t \in [-\tau, 0], \tag{5.68}$$

$$w(R,t) = 0, \tag{5.69}$$

where $c_j(w(r, t-\tau))$ is given in (5.66), w_0 is the initial history function and (5.69) is the Dirichlet boundary condition.

Slightly changing our point of view, we may consider the case that the initial condition in (5.15) is independent of θ. Then there is no reason that the final solution V^s is dependent on θ. Therefore, in this case equation (5.46) is directly reduced to (5.67). The ecological interpretation of (5.15) being independent of θ is that the reproduction of individuals takes place without any angular preference.

In comparison with (5.46), equation (5.67) represents a simpler form of population dynamics. But in what follows we can see that under some conditions the model can be formulated much simpler than (5.46) and (5.67). We can see that the final form of the model is strongly influenced by the initial condition for V^s. It is known that if the initial condition happens to be in the shape of a particular mode, then the system will vibrate that mode. Let, for instance, $b(w(r, \theta, s))$ in (5.15) be in the form of

$$b(w(r, \theta, s)) = f(s) J_1(k_{10} r) \cos\theta, \tag{5.70}$$

where $f(s)$ is a function of s.

Considering that $s = t - \tau$ is a fixed value, equation (5.29) is reduced to

$$V^{t-\tau}(R, \theta, t) = \epsilon f(s) J_1(k_{10} r) \cos\theta \exp(-k_{10}\alpha). \tag{5.71}$$

Hence the model (5.67) is reduced to

$$\frac{\partial w}{\partial t} = D_m \left(\frac{\partial^2 w}{\partial r^2} + \frac{1}{r}\frac{\partial w}{\partial r} + \frac{1}{r^2}\frac{\partial^2 w}{\partial \theta^2} \right) - d_m w + \epsilon e^{-k_{10}\alpha} f(t-\tau) J_1(k_{10} r) \cos\theta. \tag{5.72}$$

Note that the reason for considering the birth function in the form of (5.70) is that for θ and s fixed, the form of the Bessel function $J_1(x)$ for $x \in [0, k_{10} r]$ is quite similar to some birth functions used in different studies. Figure 5.1 represents such a quality. It shows a comparison between the birth function $b(w) = b_2(w)$ and the initial condition given in equation (5.70) for $\theta = 0$ and $f(s) = 1$.

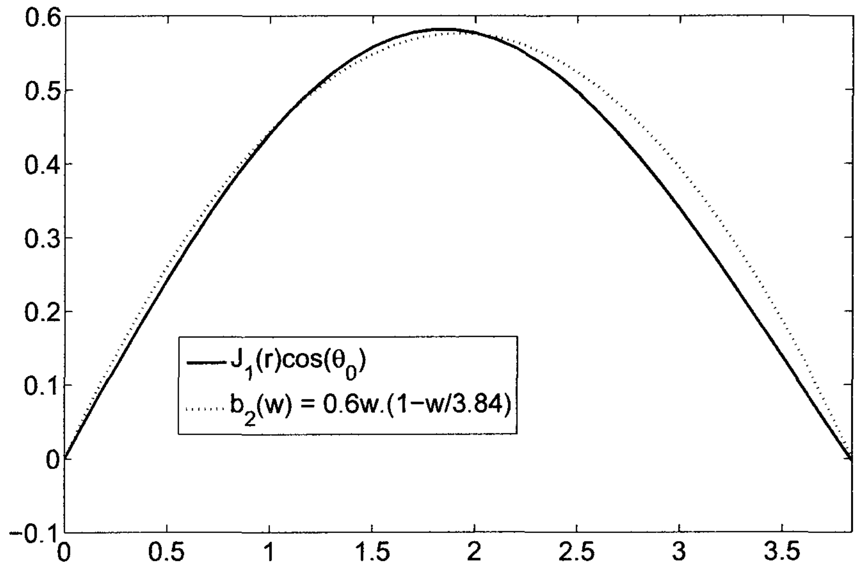


Figure 5.1: The birth function $b(w) = b_2(w)$ is quite similar to the initial condition given in equation (5.70) for $\theta_0 = 0$ and $f(s) = 1$.

In summary, we have developed the original age-structured model of single species with respect to a circular spatial domain. It should be noted that the choice of the circular domain comes from the fact that a number of experimental studies have been conducted with the same shape of domain. In general we can see that the model derivation is very dependent on the linear RD equation (5.11), the spatial domain and the boundary conditions. In the case that the domain is unbounded and two-dimensional, the same approach outlined in [165] can be used to derive the following nonlocal RD model.

$$\frac{\partial w}{\partial t} = D_m \left(\frac{\partial^2 w}{\partial x^2} + \frac{\partial^2 w}{\partial y^2} \right) - d_m w + \epsilon \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} b(w(z_x, z_y, t-\tau)) f_\alpha(x-z_x, y-z_y) dz_x dz_y, \tag{5.73}$$

where $(x, y) \in \mathbb{R}^2$, $0 < \epsilon \leq 1$. $w(x, y, t)$ represents the total matured population $u(x, y, a, t)$ at age a, time t and position x that is given by

$$w(x, y, t, a) = \int_{\tau}^{\infty} u(x, y, a, t) da.$$

The kernel function is given by $f_\alpha(x, y) = \frac{1}{\sqrt{4\pi\alpha}} e^{-\frac{x^2+y^2}{4\alpha}}$ with $\alpha = \tau D_I > 0$ and $\tau > 0$ is the maturation time. All other elements of the model are the same as described before (see Section 1.4 of Chapter 1).

Analysis of the above-mentioned models is our main goal in future studies. Specifically the traveling and stationary wave solutions of these models will be studied numerically and analytically. We believe the correct choice of the birth function $b(w)$ makes the analysis of each model more meaningful in biological and ecological contexts. On the other hand, there have been great similarities in mathematical modeling of single species and those of infectious diseases. There is a potential for employing the same methodology to derive more realistic nonlocal RD models capable of capturing new aspects of the spread of disease in a spatial domain.

5.4 Conclusions

The complexity of the biological sciences demands new research tools to understand the key elements from varied perspectives. As biology becomes more quantitative, mathematical modeling is introduced as an imperative instrument in the biological sciences. Analysis of mathematical models can reveal complex and nonlinear mechanisms that might not be evident based only on experimental observations.

The present work is an implementation of mathematical techniques to study one of the key elements of biological sciences. In particular, the appearance of waveforms is an underlying element for a large number of natural phenomena. The main contributions of the present study are not limited to the wave studies of a certain mathematical model. Instead, alternative techniques implemented in this study can be used for a wide range of models for diverse research areas.

The new generation of mathematical models has brought intense activity to different areas of biology such as ecology and epidemiology. These models are usually described by delayed nonlocal diffusive systems of differential equations. The local and global analysis of these models is the current focus of many mathematicians. The present work considers the age-structured model of single species proposed by So et al. [165]. Namely, the spatial spread of individuals is considered in a delay model by adding nonlocal and also diffusion terms.

Although the primary focus of the present work is to investigate the wave solutions of the proposed model, the problem is mostly treated for a general class of nonlocal delayed RD equations. Also, as a complementary treatment of the wave problem, detailed local and global analysis of the model is provided. This is carried out through standard techniques such as linearization, Liapunov functionals and the method of characteristics. The outcomes of the local and global analysis are encompassed in the studies of the wave solutions. There are a growing number of studies concentrated only on the traveling wavefronts. An essential aspect of the present work is that it takes into account both stationary and traveling wave solutions. The study of stationary wave pulses and wavefronts can play a crucial role in distinct biological occurrences. Of particular interest it is employed to capture the dynamics of single species populations in the spatial domain. The phase-plane stationary solutions are directly obtained by solving the corresponding wave equation. Analysis of phase-plane solutions through the energy functions method indicates the presence of stationary wave solutions. The other methods such as asymptotic expansion methods are aimed to provide approximations of traveling wave solutions. The final step in the present work is devoted to development of the model with respect to a two-dimensional domain. Although model development is carried out by a number of researchers, the choice of the spatial domain makes a huge difference in the final form of the model. It is felt the model development with respect to circular spatial domains harmonizes with the underlying principles of the population dispersal.

In summary, the results of this study contributes to the existing literature in three important respects. First it takes into account the local stability analysis of the population model. Secondly, it demonstrates how alternative techniques are utilized to deal with traveling and stationary wave solutions. Thirdly, it makes an effort to develop the population model according to the spatial domain used in a number of laboratory experiments.

Future studies might include a deeper analysis of wave solutions with respect to overcompensating density dependent birth functions with Allee effect. In particular, considering such birth function gives rise to bistability and crossing bistability, which require stronger techniques to obtain accurate approximations of the wave solution. The differential transform method presented in this study is a novel approach that is intended to be further developed. We believe the reduction of the Cauchy problem of the wave equation to a nonlinear system of equations takes the entire problem to a distinct area of applied mathematics. This provides the opportunity of treating the problem with different techniques available for solving homogeneous nonlinear systems of equations. As previously mentioned, there is the potential to employ the Melnikov method to investigate the existence of slowly traveling wave pulses. Then a slightly perturbed stationary wave pulse may begin to slowly travel in the spatial domain. This is of particular interest since the recent literature is mostly focused on the existence of traveling wavefronts with wave speeds grater than a minimal value. The numerical experiments performed in this study should be continued with respect to the full nonlinear population model. The key elements are the assessment of the traveling and stationary wave occurrences in the spatial domain, investigation of the traveling wave stabilities, estimation of the wave speed and detection of wave direction. Also the numerical analysis of the generalized model is considered as an objective of future work.

THE END

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