



Mathematical population dynamics models in deterministic and stochastic environments

Trong Hieu Nguyen

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Présentée par

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STOCHASTIQUE

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Résumé

Résumé: Dans ce travail de thèse, nous étudions des modèles mathématiques de la dynamique des populations en environnements déterministe et stochastique. Pour les environnements déterministes, nous considérons trois modèles. Le premier est un modèle intra-gilde prenant en compte des effets d'un environnement spatial hétérogène avec une migration rapide des individus entre les différents sites. Le deuxième est un modèle de pêche dans une zone constituée d'une aire marine protégée où la pêche est interdite et d'une zone où la population de poissons est pêchée. Enfin le troisième est un modèle prédateur-proie considérant une proie et deux prédateurs avec des réponses fonctionnelles de Beddington-DeAngelis. Pour les environnements stochastiques, nous étudions un modèle épidémique SIRS et un modèle prédateur-proie en prenant en compte un bruit télégraphique. Nous étudions le comportement dynamique de ces modèles et nous recherchons les conditions de maintien ou de disparition des espèces modélisées.

Mots clés: Prédation intra-gilde, migration rapide, bancs de poisson, zone de protection marine, système à trois niveaux, équation de Lotka-Volterra, système prédateur-proie, modèle SIRS, bruit télégraphique.

Abstract

Abstract: In this thesis, we consider mathematical population dynamics models in deterministic and stochastic environments. For deterministic environments, we study three models: an intraguild model with the effects of spatial heterogeneous environment and fast migration of individuals; a fishery model with Marine Protected Area where fishing is prohibited and an area where the fish population is harvested; a predator-prey model which has one prey and two predators with Beddington-DeAngelis functional responses. For stochastic environments, we study SIRS epidemic model and predator-prey models under telegraph noise. We try to present the dynamical behavior of these models and show out the existence or vanishing of species in the models.

Keywords: Intraguild predation, fast migration, fish school, marine protected area, three level system, Lotka-Volterra equation, predator-prey system, SIRS model, telegraph noise.

Chapter 1

Introduction

1.1 Population dynamics

1.1.1 Single species growth

The exponential growth model

In 1798 Malthus published a book entitled *An Essay on the Principle of Population* [94]. In this book he investigated the simplest population model of single species

$$\frac{dx}{dt} = bx - dx, \quad (1.1.1)$$

in which b and d are *per capita* birth and death rate, $x(t)$ is the population size of the species at time t . The equation (1.1.1) can be written more succinctly as

$$\frac{dx}{dt} = rx, \quad (1.1.2)$$

where $r = b - d$ is known as the intrinsic growth rate of species or the *Malthusian parameter*. If $x(0) = x_0$ is the size of population at the initial time, the equation (1.1.1) has solution $x(t) = x_0 e^{rt}$. The growth rate r is positive only if birth rate is higher than death rate and then $x(t) = x_0 e^{rt} \rightarrow \infty$ as $t \rightarrow \infty$. The model (1.1.1) is suitable for the growth of species, like bacteria in a nutrient-unlimited supplied environment.

The Logistic model

The fact that many resources are available only in limited quantities, it is impossible to have unlimited exponential growth of any population over the long run. Moreover, a large population implies fewer resources for each individual. This reason leads to logistic model which is first introduced by Verhulst [143] and later studied further by R. Pearl and L. J. Reed [114]

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right), \quad r, K > 0. \quad (1.1.3)$$

It is observed that $\dot{x} \approx rx$ if x is small, and $\dot{x} \approx 0$ when x is near K . It means that for small x the population dynamics is just the exponential growth, when x is near K the size of population hardly changes. Simultaneously, if x is large, the individuals of the species compete with each other for fewer resources.

By solving equation $\dot{x} = 0$, we see that the equation (1.1.3) has two steady states (also called equilibrium or rest point) $x^* = 0$ and $x^* = K$. With population size at time $t = 0$ is x_0 , the solution of model (1.1.3) is obtained as follows

$$x(t) = \frac{Kx(0)e^{rt}}{K + x(0)(e^{rt} - 1)}. \quad (1.1.4)$$

From the equation (1.1.3) and solution (1.1.4), we see that if $0 < x < K$ then $\dot{x} > 0$ and $x(t)$ increases asymptotically to K , if $x > K$, $\dot{x} < 0$ and $x(t)$ decreases asymptotically to K as $t \rightarrow \infty$. Hence K is called *carrying capacity* of the environment and it is the population size of species that available resources can support.

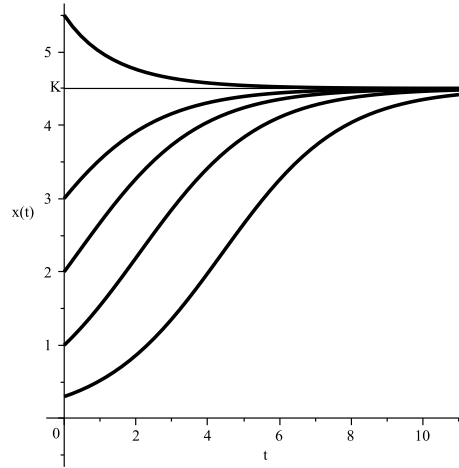


Figure 1.1: Solutions of logistic model

Other single species models have been used by many ecologists, for example:

$$\dot{x} = x\left(b + \frac{a-x}{1+cx}\right) \quad (\text{Pianka 1972})[117],$$

$$\dot{x} = rx\left(1 - \left(\frac{x}{K}\right)^\theta\right) \quad (\text{Gilpin and Ayala 1973})[61],$$

$$\dot{x} = rx\left(\frac{I}{x} - C - bx\right) \quad (\text{Schoener 1973})[129],$$

$$\dot{x} = -ax \log\left(\frac{x}{K}\right) \quad \text{Gompertz's model (Swann and Vincent 1977)}[135],$$

where $a, b, c, r, \theta, K, I, C$ are positive constants.

Table 1.1: Organizing ecological interactions.

Effect on species 1	Effect on species 2	Type of interaction
0	0	Neutralism
—	—	Competition
+	—	Predation
+	+	Mutualism
+	0	Commensalism
0	—	Amensalism

1.1.2 Biological interaction

In ecology, biological interactions can involve individuals of the same species (intraspecific interactions) or individuals of different species (interspecific interactions). Here we concentrate the interaction between species (interspecific interactions), they are categorized as either neutralism, competition, predation/parasitism, mutualism/symbiosis, commensalism or amensalism (see Table 1.1). In this section, we are interested in competition, predation and mutualism.

Competition is a negative interaction that occurs when organisms of different species use the same resource(s) at the same time and the growth rate of each species is decreased. Examples of competition are *Asterionella formosa* and *Synedra ulna* [141], ants and rodents near Portal, Arizona [142].

Predation is most commonly considered to be an interaction where an organism (predator) consumes all or part of another living organism (its prey) thereby benefiting itself, but reducing the growth of the prey. For examples, lynx prey upon hares [105], cheetahs and wild dogs kill gazelles [142].

Mutualism is the positive interaction that species provide resources or services to each other and each species's growth rate is enhanced. One example of mutualism is the relationship between *Labroides dimidiatus* (cleaner fish) and *Hemigymnus melapterus* (client fish) [142].

1.1.3 Lotka-Volterra systems

The general Lotka-Volterra equation

The classical Lotka-Volterra model is a pioneering work of Lotka and Volterra in the beginning of twentieth century [25, 105, 137]. The general Lotka-Volterra equation for n population is of the form

$$\dot{x}_i = x_i(r_i + \sum_{j=1}^n a_{ij}x_j) \quad i = 1, \dots, n. \quad (1.1.5)$$

The x_i denote densities of i -th species, the growth rate r_i are intrinsic growth (or decay) rates and a_{ij} present the effect of the j -th species upon the i -th species. The matrix $A = (a_{ij})$, of which the elements are the interaction coefficients, is called the *interaction matrix*. Since populations can not be negative, the state space is the nonnegative orthant $\mathbb{R}_+^n = \{x = (x_1, \dots, x_n) \in \mathbb{R}^n : x_i \geq 0 \text{ for } i = 1, \dots, n\}$.

In this model, the sign pattern of (a_{ij}, a_{ji}) describes the interaction between the i -th species and the j -th species. If the sign is $(-, -)$ or $(+, +)$, then the relationship is competition or mutualism respectively. For predator-prey, it is $(+, -)$ or $(-, +)$. Some models of these relationship will be introduced in the next section.

The competition model

Let us consider a model of two competing species. They compete for the same limited resource or in some way inhibit each other's growth. This model is described by basic 2-species Lotka-Volterra competition equation with each species 1 and 2 having logistic growth in the absence of the other. It is of the form

$$\begin{cases} \dot{x} = x(a - bx - cy) \\ \dot{y} = y(d - ex - fy), \end{cases} \quad (1.1.6)$$

in which x, y denote densities of species 1 and 2 respectively; a, b, c, d, e and f are all positive constants [25, 52]. The relative sizes of c, e determine the competitiveness of each species.

The system (1.1.6) has 4 equilibria $(0, 0), (0, \frac{d}{f}), (\frac{a}{b}, 0)$ and $(x^*, y^*) = (\frac{af - cd}{bf - ce}, \frac{bd - ae}{bf - ce})$. Figure 1.2 shows the all possibilities of solutions of (1.1.6). We summarize the result of the model (1.1.6) as follows:

- $af - cd > 0, bd - ac > 0$. In this case there is a positive steady state (x^*, y^*) in the first quadrant and it is asymptotically stable. All positive solutions of (1.1.6) tend to (x^*, y^*) (Figure 1.2(a)). The competition between two species is not too strong, two species can coexist.
- $cd - af > 0, ac - bd < 0$. (x^*, y^*) is a positive steady state but it is saddle point. A separatrix divides the first quadrant into two regions, one containing initial

points for which orbits tend to $(\frac{a}{b}, 0)$, and the other containing initial points for which orbits tend to $(0, \frac{d}{f})$. The survival of species depends on initial state (Figure 1.2(b)).

- $af - cd > 0, ac - bd > 0$. There is no positive steady state. $(\frac{a}{b}, 0)$ is an asymptotically stable and all solutions tend to it (Figure 1.2(c)). The species 1 wins and the species 2 will be extinct when $t \rightarrow \infty$.
- $cd - af > 0, bd - ac > 0$. In this case there is no interior steady state, all orbits tend to $(0, \frac{d}{f})$ (Figure 1.2(d)). Interspecific competition of species 2 dominates the species 1. Species 2 wins and drives the species 1 to extinction.

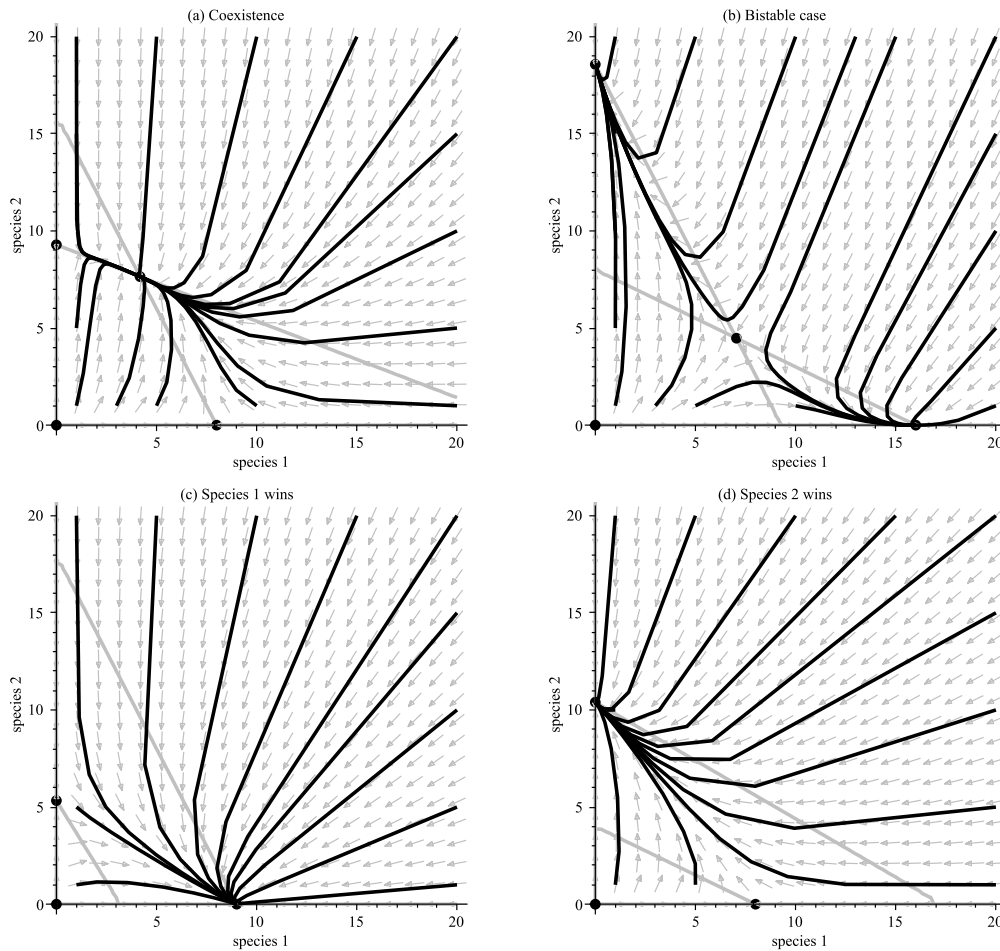


Figure 1.2: Orbits of model (1.1.6) in four cases of coefficients

The mutualism model

We study a model in which the two species benefit from the presence of the other. We incorporate limited carrying capacities for both species. A simple two-species

mutualism model is given by the next system

$$\begin{cases} \dot{x} = x(a - bx + cy) \\ \dot{y} = y(d + ex - fy), \end{cases} \quad (1.1.7)$$

where a, b, c, d, e and f are all positive constants. x, y are densities of species 1 and 2 respectively [25, 105]. The constants c and e denote the coefficients interaction between the two species that increase the densities of species 1 and 2 respectively.

Depending on the relationship between bf and ce , dynamical behavior of solutions have two possibilities.

- If $bf > ce$ then (1.1.7) has one positive steady state $(x^*, y^*) = (\frac{af+cd}{bf-ce}, \frac{ae+bd}{bf-ce})$ and all interior orbits converge to (x^*, y^*) (Figure 1.3(a)). Moreover the inequalities $x^* > \frac{a}{b}$ and $y^* > \frac{d}{f}$ mean that the species converge to populations exceeding their carrying capacities.
- When $bf < ce$, the mutualistic effects are greater than the self-limiting terms in the per capita growth rates. In this case (1.1.7) has no positive steady state, unbounded growth occurs and all interior orbits diverge to infinity (Figure 1.3(b)).

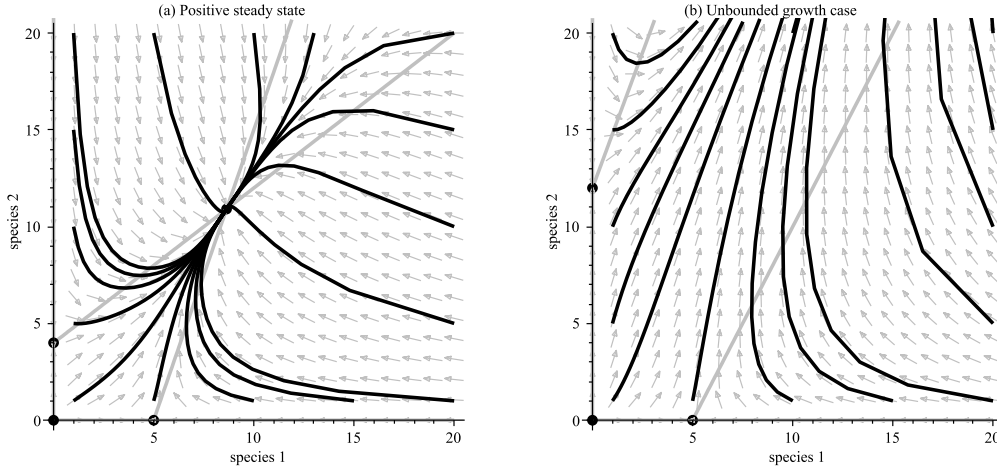


Figure 1.3: Orbits of model (1.1.7)

The Predator-prey model

In 1926 Vito Volterra wrote a paper, entitled "Fluctuations in the abundance of a species considered mathematically" [16], to explain the change of the amount of fish in the Adriatic. He denoted by x the density of the prey fishes, also by y that of predators. He assumed that the growth rate of prey is a positive constant a in

the absence of the predator and the predators will decay to zero exponentially with Malthusian parameter c if there exists no prey. This gives the equations

$$\begin{cases} \dot{x} = x(a - by) \\ \dot{y} = y(-c + dx), \end{cases} \quad (1.1.8)$$

where the parameter b represents the attack rate of predators, the rate $\frac{d}{b}$ represents the conversion efficiency [52, 105]. At the same time this model was also constructed by Lotka in the context of chemical kinetics, so it is called Lotka-Volterra model.

(1.1.8) is rewritten as

$$\frac{\dot{y}(a - by)}{y} = \frac{\dot{x}(-c + dx)}{x}.$$

This equation can be integrated directly. Then any solution (x, y) of the equation (1.1.8) satisfies the identity

$$V(x, y) = -c \ln x - a \ln y + dx + by = h,$$

where the constant $h = V(x_0, y_0) = -c \ln x_0 - a \ln y_0 + dx_0 + by_0$ is determined by initial conditions (x_0, y_0) and system parameters. Thus every orbit of (1.1.8) is given implicitly by an equation $V(x, y) = h$. They are periodic orbits with period T , in which time averages of $x(t)$ and $y(t)$ are constant and satisfy $\frac{1}{T} \int_0^T x(t) dt = \frac{c}{d}$, $\frac{1}{T} \int_0^T y(t) dt = \frac{a}{b}$.

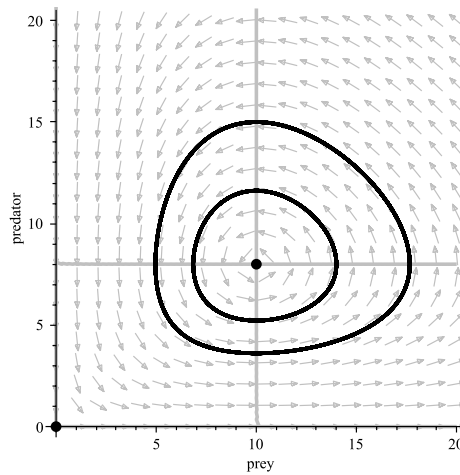


Figure 1.4: Orbits of Lotka-Volterra predator-prey model (1.1.8).

In (1.1.8) the growth rate of prey decreases linearly as a function of the predator density. In many model the term bxy is replaced by some explicit forms for the predator functional response

$$\alpha y(1 - e^{\beta x}) \quad (\text{Ivlev (1961)})[72],$$

$$\frac{\alpha xy}{x + \beta} \quad (\text{Holling (1965)})[68],$$

$$\alpha y x^\beta \quad (1 \geq \beta > 0) \quad (\text{Rosenzweig (1971)})[125],$$

$$\frac{\theta xy}{\alpha + \beta x + \gamma y} \quad (\text{Beddington (1975), DeAngelis (1975), independently})[23, 48],$$

where α, β, γ and θ are positive constants.

There are many attempts to apply the Lotka-Volterra predator-prey model to real-world oscillatory phenomena. Figure 1.5 show the data of the population size of lynx and snow hare. The data is collected by The Hudson Bay Company [86, 105]. The orbit in Figure 1.5(a) is a more or less closed curve and the oscillation of population size of two species are presented by Figure 1.5(b).

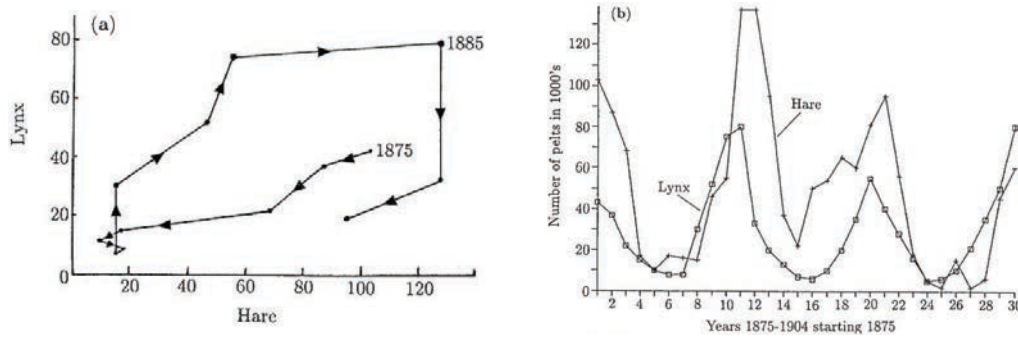


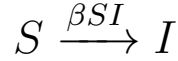
Figure 1.5: Realistic data of lynx-hare population. (a) Phase plane plot of the data. (b) Oscillation of population size.

1.2 Mathematical modelling of infectious disease

Infectious diseases can be classified into two broad categories: those caused by viruses and bacteria are microparasitic diseases, and those due to worms are macroparasitic. In this section we concentrate on infectious diseases where individuals are infected by pathogen microorganisms (like, for instance, viruses, bacteria, fungi or other microparasites). Some well known examples of such infectious diseases are: Influenza, SARS, Reublla, AIDS, Ebola ... (Viral infectious diseases); Cholera, Plague, Typhus, Leprosy... (Bacterial infectious diseases); Malaria, Taeniasis... (Parasitic infectious diseases);...

Mathematical modelling of infectious diseases is a tool to provides understanding of the underlying mechanisms that influence the spread of disease, explains epidemiological phenomena, and predict the future course in order to control an epidemic. Here, we summarize some of the simple classical models for microparasitic infections. In these models we assume the population has no births, deaths, migration and the total population size is a constant N . We also assume that every individual has an equal chance to meet any other member of the population and these interactions are random.

The SI model



We consider the spread of a disease in a population. We assume that the size of population is N and fixed. The population has only two class of individuals: susceptible S and infected class I . β is the disease transmission (infection) rate. So we have the model

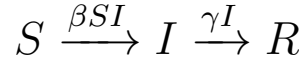
$$\dot{I} = \beta SI. \quad (1.2.1)$$

The SI model is the simplest model of an infectious disease. By $S + I = N$, then (1.2.1) can be written as follows

$$\dot{I} = \beta NI \left(1 - \frac{I}{N}\right)$$

This is a logistic equation with carrying capacity N . Hence, with initial value $I(0) > 0$, I approaches to N . It means that no matter how small the initial population of infectives, all individuals of population will become infected.

The SIR model



The first paper about the SIR model was published by Kermack and McKendrick in 1927. Here, the population is divided into three classes: the susceptibles, S , who can catch the disease; the infectives, I , who have the disease and can transmit it; and the removed class, R , namely, those who have either had the disease, or are recovered, immune or isolated until recovered [105]. Transitions between classes describe the course of transmission and recovery with rate constants β and γ . The model is then

$$\begin{cases} \dot{S} = -\beta SI \\ \dot{I} = \beta SI - \gamma I \\ \dot{R} = \gamma I. \end{cases} \quad (1.2.2)$$

Adding three equations of (1.2.2), we have $\dot{S} + \dot{I} + \dot{R} = 0$. Thus, $S + I + R = N = \text{const}$, where N is the total size of the population. We see that R is determined once S and I are known, and we can drop the R equation from (1.2.2), leaving the system of two equations

$$\begin{cases} \dot{S} = -\beta SI \\ \dot{I} = \beta SI - \gamma I. \end{cases} \quad (1.2.3)$$

Let us consider an epidemic problem in a population where only a few individuals are infected at the initial time. The initial conditions are $S(0) = S_0 \approx N$, $I(0) = I_0 = N - S(0) \approx 0$, $R(0) = R_0 = 0$. From (1.2.3) we have

$$\frac{\dot{S}}{\dot{I}} = \frac{-\beta SI}{(\beta S - \gamma)I}.$$

It follows $I + S - \frac{\gamma}{\beta} \ln S = \text{const} = I_0 + S_0 - \frac{\gamma}{\beta} \ln S_0$. Since equation $\dot{I} = (\beta S - \gamma)I$, it shows that $\dot{I} > 0$ if and only if $S > \frac{\gamma}{\beta}$. Hence I increases so long as $S > \frac{\gamma}{\beta}$, but since S always decreases, I ultimately decreases and tend to 0. I gets $I_{\max} = N - \frac{\gamma}{\beta} + \frac{\gamma}{\beta} \ln \left(\frac{\gamma}{\beta S_0} \right)$ (Figure 1.6). If $S_0 < \frac{\gamma}{\beta}$, I decreases to 0 and this is no epidemic case. While if $S_0 > \frac{\gamma}{\beta}$, I firstly increases to I_{\max} and then decreases to 0, this is epidemic case.

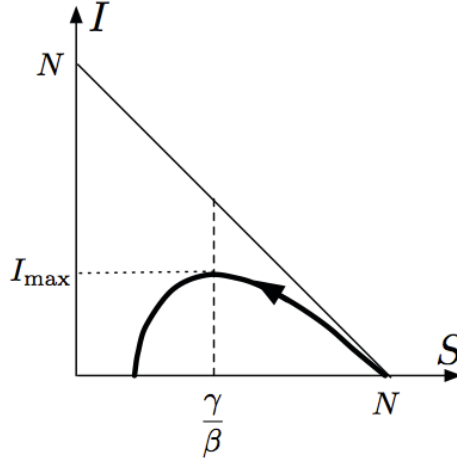


Figure 1.6: An epidemic trajectory of model (1.2.3).

The quantity $S_0 \frac{\beta}{\gamma} \approx N \frac{\beta}{\gamma} =: \mathcal{R}_0$ is a threshold quantity. \mathcal{R}_0 is called the *basic reproduction number*. The definition of the basic reproduction number \mathcal{R}_0 is that it is the number of secondary infections caused by a single infective introduced into a wholly susceptible population of size $N \approx S_0$ over the course of the infection of this single infective [25]. If $\mathcal{R}_0 > 1$, an epidemic occurs, while if $\mathcal{R}_0 < 1$, the infection dies out.

In [105] Murray presented an interesting application of the SIR model. It is the basis of influenza epidemic data in an English boarding school published in 1978 by The British Medical Journal. The epidemic happened from 22nd January to 4th February 1978. The size of population $N = 763$ boys in the school were infected and are represented by dots in Figure 1.7. The curves in the figure represent trajectory of the SIR model fitted to the data.

The SIRS model

$$S \xrightarrow{\beta SI} I \xrightarrow{\gamma I} R \xrightarrow{\alpha R} S$$

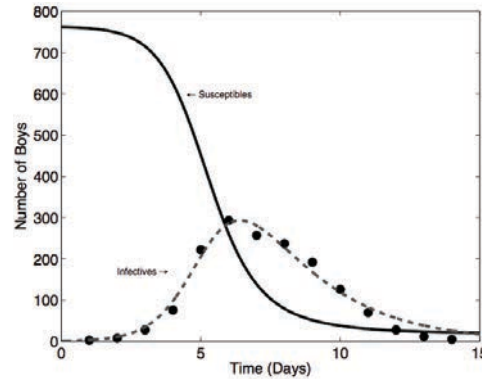


Figure 1.7: An influenza epidemic in an English boarding school in 1978. It is a realistic example of the SIR model.

Let us again consider the SIR model. We assume that individuals of the removed class to be free of infection and become susceptible again. The parameter α represents the specific rate of immunity loss of population in R class and rejoin S class. Then the SIRS model is given by the next system [86]

$$\begin{cases} \dot{S} = -\beta SI + \alpha R \\ \dot{I} = \beta SI - \gamma I \\ \dot{R} = \gamma I - \alpha R. \end{cases} \quad (1.2.4)$$

The system (1.2.5) have two equilibria: disease free equilibrium $(0, 0, 0)$ and endemic equilibrium $(S^*, I^*, R^*) = (\frac{\gamma}{\beta}, \frac{N - \frac{\gamma}{\beta}}{1 + \frac{\gamma}{\alpha}}, \frac{N - \frac{\gamma}{\beta}}{1 + \frac{\alpha}{\gamma}})$. In order to exist the positive endemic equilibrium, the following condition must hold:

$$\mathcal{R}_0 = N \frac{\beta}{\gamma} > 1$$

In further studying the SIRS model, we note that $\dot{S} + \dot{I} + \dot{R} = 0$, the sum $S + I + R = N$ and it is a constant of population size. So that for convenience the removed class R can always be eliminated. The reduction of the equation (1.2.4) is then

$$\begin{cases} \dot{S} = -\beta SI + \alpha(N - S - I) \\ \dot{I} = \beta SI - \gamma I. \end{cases} \quad (1.2.5)$$

Depending on the value of basic reproduction number, we have two cases. If $\mathcal{R}_0 = N \frac{\beta}{\gamma} < 1$, (1.2.5) has no positive endemic equilibrium, I decreases and all orbits tend to $(N, 0)$ (Figure 1.8(a)). If $\mathcal{R}_0 = N \frac{\beta}{\gamma} > 1$, all orbits of (1.2.5) approach to endemic equilibrium (Figure 1.8(b)). It means that epidemic case will happen when basic reproduction number $\mathcal{R}_0 > 1$. It is in agreement with the condition for

an epidemic to occur in the SIR model. In epidemic case, I of the SIR model tend to 0 but I of the SIRS model tend to $I^* > 0$, the SIRS model always have infected individuals.

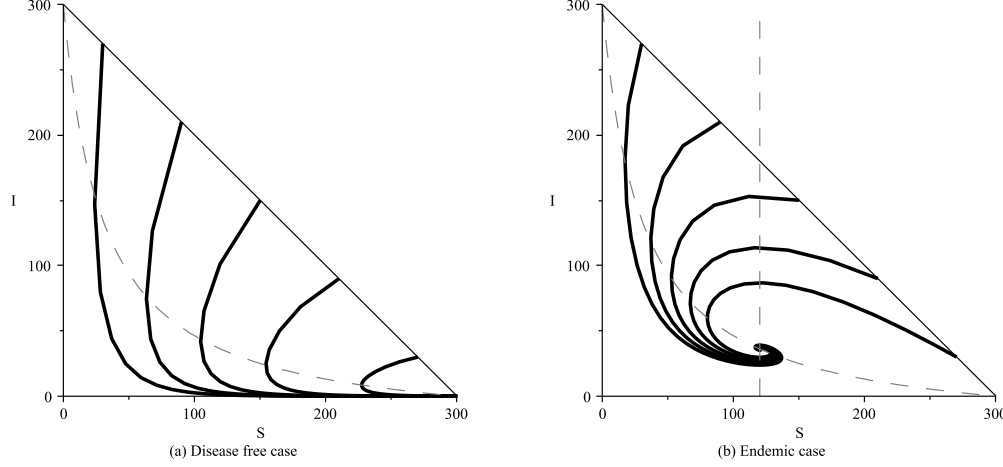


Figure 1.8: Orbits of the SIRS model (1.2.5)

In this section we assume that the models have no demography. Nowadays many kinds of epidemic models, with or without demography, have been proposed and studied. We can find some of them in [21, 25, 39, 105].

1.3 Models and obtained results

In this thesis we give out some ecosystem models and concentrate on dynamical behavior of these models. So we can see the existence or vanishing of species of ecological systems, and when they are dissipative, persistent, permanent. A species with population size $x(t)$ with respect to time t is said to be dissipative if $\limsup_{t \rightarrow \infty} x(t) < \delta$ where $\delta = \text{const} > 0$ and to be (weak) persistent if $\limsup_{t \rightarrow \infty} x(t) > 0$. Persistence, however, does not ensure survival of a species in a biological sense. Permanence implies the survival of all species which exist initially. A ecological system is said to be permanent if there exist a compact set K in the interior of the state space such as all orbits in the interior end up in K , i.e. there exist $\delta_1, \delta_2 > 0$ such that $\delta_1 < \liminf_{t \rightarrow \infty} x(t) < \limsup_{t \rightarrow \infty} x(t) < \delta_2$ [25, 67, 137].

In chapter 2 we investigate effects of spatial heterogeneous environment and fast migration of individuals on coexistence of the intraguild predation (IGP) dynamics. We present a two-patch model. We assume that on one patch two species compete for a common resource, and on the other patch one species can capture the other one for the maintenance. We also assume IGP individuals are able to migrate between two patches and the migration process acts on a fast time scale in comparison with demography, predation and competition processes. This chapter show that under certain conditions the heterogeneous environment and fast migration can lead to coexistence of the two species.

In chapter 3 we consider a fishery model with two sites: (1) a Marine Protected Area (MPA) where fishing is prohibited and (2) an area where the fish population is harvested. We assume that fish can migrate from MPA to fishing area at a very fast time scale and fish spatial organisation can change from small to large clusters of school at a fast time scale. The growth of the fish population and the catch are assumed to occur at a slow time scale. The complete model is a system of 5 ordinary differential equations with three time scales. We take advantage of the time scales using aggregation of variables methods to derive a reduced model governing the total fish density and fishing effort at the slow time scale. We analyze this aggregated model and show that under some conditions, there exists an equilibrium corresponding to a sustainable fishery. Our results suggest that in small pelagic fisheries the yield is maximum for a fish population distributed among both small and large clusters of school.

We study a predator-prey model which has one prey and two predators with Beddington-DeAngelis functional responses in chapter 4. Firstly, we establish a set of sufficient conditions for the permanence and extinction of species. Secondly, the periodicity of positive solutions is studied. Thirdly, by using Liapunov functions and the continuation theorem in coincidence degree theory, we show the global asymptotic stability of such solutions. Finally, we give some numerical examples to illustrate the behavior of model.

Some population models with the effect of random environment were studied in chapter 5. It is structured into two sections. In the first section we present the Kernack - MacKendrick model under telegraph noise. The telegraph noise switches at random between two SIRS models. We give out conditions for the persistence of the disease and the stability of a disease free equilibrium. We show that the asymptotic behavior highly depends on the value of a threshold λ which is calculated from the intensities of switching between environmental states, the total size of the population as well as the parameters of both SIRS systems. According to the value of λ , the system can globally tend towards an endemic case or a disease free case. The aim of this chapter is also to describe completely the omega-limit set of all positive solutions to the model. Moreover, the attraction of the omega-limit set and the stationary distribution of solutions will be pointed out.

In the second section of chapter 5, we consider Lotka-Volterra predator-prey systems with the effect of telegraph noise. For predator-prey system with carrying capacity of environment, we focus on persistence of the predator and thus we look for conditions that allow persistence of the predator and prey community. We also determine the subset of omega-limit set of this system. For predator-prey model with the absence of carrying capacity, it is proved that under the influence of telegraph noise, all positive trajectories of such a system always exile from any compact set of $\text{int}\mathbb{R}_+^2$ with probability one if two rest points of the two systems do not coincide. In case where they have the rest point in common, the trajectory either leaves from any compact set of $\text{int}\mathbb{R}_+^2$ or converges to the rest point. The exile of the trajectories from any compact set means that the system is neither permanent nor dissipative.

Chapter 2

Spatial heterogeneity, fast migration and coexistence of Intraguild Predation Dynamics

2.1 Introduction

In this chapter we present paper [112]. It is well-known that interactions between species are usually categorized as either competition (negative effects on each other), predation/parasitism (one got positive effect and the other got negative effect), mutualism (positive effects on each other), commensalism (one got positive effect and the other got no effect) or amensalism (one got negative effect and the other got no effect). Intraguild predation (IGP) is a combination of the first two, that is, the killing and eating species that use similar resources and are therefore potential competitors [124]. Thus, broadly speaking, cannibalism is considered as a form of IGP unless there is a distinct ontogenetic niche shift that differentiates the resource profile of cannibals and their victims [146]. For example, most spiders are generalist predators that feed on a variety of prey items such as mosquitoes and flies, making them members of the same guild. However, spiders also eat other spiders, we count this cannibalism as intraguild predation. IGP commonly involves larger individuals feeding on smaller individuals [122]. We call the victim intraguild prey (IGprey) and the predator intraguild predator (IGpredator). IGP is common in nature and is found in a variety of taxa [121, 122, 123, 124, 145]. It differs from classical predation because the act reduces potential exploitation competition. Thus, its impact on population dynamics is much more complex than either competition or predation alone. One characteristic of IGP is the simultaneous existence of competitive and trophic interactions between the same species.

Theoretical models predict that coexistence of IGpredator and IGprey is difficult, because IGprey experience the combined negative effects of competition and predation [69]. In systems with competition only, IGprey suffers no predation. In standard predator-prey interactions without competition, IGprey suffer no exploita-

tive competition from the IGpredator. Thus, IGP is more stressful for the intermediate consumer (IGprey) than either exploitative competition or trophic interaction alone.

The theoretical difficulty in explaining IGP persistence and its observed ubiquity have identified IGP as an ecological puzzle [69]. This led to a series of studies in order to resolve the puzzle. These studies have considered factors such as top predators (food web topology) [149], size structure [24, 93, 106], habitat segregation [93], metacommunity dynamics [101], intraspecific predation [49], and adaptive behavior [80, 81, 82].

Here, we investigate an IGP model in a two-patch environment. We assume that on one patch is pure exploitation competition, and on the other one IGpredator can capture IGprey for its maintenance. This considered scenario can potentially occur in some ecological systems. For instance, on a given patch with an abundant resource the interaction of species is more likely to be exploitation competition, while on another patch with a limit of resource one species is more likely to reduce the risk for shared resource by feeding on its competitors [45]. Aquatic invertebrates and fishes tend to prey on eggs and larvae of their resource competitors (see examples in [124]). In some populations [122], larger individuals feed on smaller individuals. Therefore, one can imagine complexity of environment may lead to the fact that individuals can (or cannot) encounter eggs, larvae and juveniles of their resource competitors (example includes niche and refuges), the predation can (or cannot) happen. The authors in [75] showed that habitat structure could reduce encounter rates between IGpredator and IGprey.

In the current contribution, we assume a non-coexistence of species locally. In the competition patch, we suppose that IGpredator is the superior exploitation competitor, i.e. without migration IGpredator out-competes IGprey. In the predation patch, we suppose that IGpredator is the inferior one so that IGpredator mainly capture IGprey in order to maintain. Moreover IGprey has a good tactics to exploit resource as well as to avoid the risk of IGpredator. This leads to the fact that without migration IGprey drives IGpredator out. Both patches are connected by density-independent migration of individuals of both IGpredator and IGprey. It is assumed that migration is fast in comparison with competition and predation in the local patches. In this work, we are going to investigate whether spatial heterogeneous environment and fast migration between patches lead to coexistence of IGP system.

We consider a fast migration in comparison with demography and interaction of species. In fact, many ecological systems highlight that migration occurs on a fast time scale relative to competition. For instance, in long lived organisms such as trees gene flow through pollination or migration can take place at a much faster time scale than selection process [58]. In host-parasite systems (in which the individual host is the patch), the interplay between within-patch and among-patch evolutionary dynamics drives the evolution of intermediate levels of virulence [88]. The authors in [103] proposed a mathematical model of zooplankton moving in the water column with food-mediated fast vertical migrations. This work showed that

fast vertical migration could enhance ecosystems stability and regulation of algal blooms. Another example can be found in [104] where authors study a model of fast-moving zooplankton capable of quick adjustment of grazing load in the water column and argue that it could be a generic self-regulation process in nature. Yet the author in [4] investigated the case where migration, demography and interaction of species act on the same time scale in an IGP model. It is shown that this migration mode can allow IGP species to coexist. We therefore consider the IGP model including the two time scales.

Taking advantage of these two time scales, we are able to use aggregation methods that allow us to reduce the dimension of the complete model and to derive a global model at the slow time scale governing the total species densities [10, 11, 15]. For aggregation of variables methods, we also refer to some investigations [73, 74]. Some applications of the aggregation method to population dynamics can be found in [13, 99, 108] and [120].

This chapter is organized as follows. Section 2.2 shows the mathematical model. In Section 2.3, we present reduction of the model. It is structured into two subsections. Subsection 2.3.1 presents the study of fast equilibrium. Subsection 2.3.2 is devoted to aggregated model. The results are discussed in Section 2.4. The last section 2.5 is about conclusion and perspectives.

2.2 Model

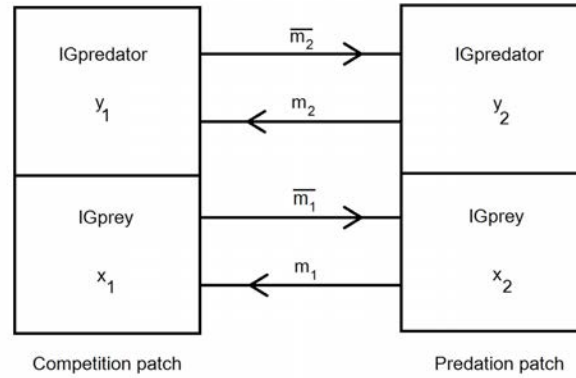


Figure 2.1: IGpredation on two patches. IGpredator compete with IGprey on patch 1 or else competition patch. The system is predation on patch 2 or else predation patch.

We consider an IGP model in a two-patch environment. We assume there is an abundant resource on patch 1 therefore IGpredator and IGprey compete with

each other for the common resource. A classical Lotka-Volterra competition model is used in order to represent this competition dynamics. In patch 2, it is assumed that IGpredator is the inferior exploitation competitor so that IGpredator mainly capture IGprey to maintain [45, 122, 124]. A classical predator-prey model is used to represent this predation dynamics. Both patches are connected by migration of IGP individuals (see Figure 2.1). We further assume the migration process acts on a fast time scale than the demography, the competition and predation processes in the two local patches. According to these assumptions, the complete system reads as follows:

$$\begin{cases} \frac{dx_1}{d\tau} = (m_1x_2 - \overline{m}_1x_1) + \varepsilon r_{11}x_1 \left(1 - \frac{x_1}{K_{11}} - a_{12}\frac{y_1}{K_{11}}\right) \\ \frac{dx_2}{d\tau} = (\overline{m}_1x_1 - m_1x_2) + \varepsilon r_{12}x_2 \left(1 - \frac{x_2}{K_{12}}\right) - \varepsilon bx_2y_2 \\ \frac{dy_1}{d\tau} = (m_2y_2 - \overline{m}_2y_1) + \varepsilon r_{21}y_1 \left(1 - \frac{y_1}{K_{21}} - a_{21}\frac{x_1}{K_{21}}\right) \\ \frac{dy_2}{d\tau} = (\overline{m}_2y_1 + m_2y_2) + \varepsilon y_2(-d + ebx_2). \end{cases} \quad (2.2.1)$$

where x_i and y_i are the densities of IGprey and IGpredator in patch i , $i \in \{1, 2\}$. r_{11} and r_{21} represent the growth rates of IGprey and IGpredator in patch 1. K_{11} and K_{21} are the carrying capacities in the competition patch of IGprey and IGpredator, respectively. a_{12} and a_{21} represent the competition coefficients showing the effect of IGpredator on IGprey and of IGprey on IGpredator. r_{12} and K_{12} are respectively the intrinsic growth rate and the carrying capacity of IGprey in patch 2. b is predation capture rate, e is the parameter related to predator recruitment as a consequence of predator-prey interaction. d is natural mortality rate of the IGpredator on the predation patch. For the IGprey, parameter m_1 is the per capita migration rate from the predation patch to the competition patch, and \overline{m}_1 , from the competition patch to the predation patch. For the IGpredator, parameter m_2 is the per capita migration rate from the predation patch to the competition patch, and \overline{m}_2 , from the competition patch to the predation patch. Parameter ε represents the ratio between two time scales $t = \varepsilon\tau$, t is the slow time scale and τ is the fast one. In this chapter, we are interested in an asymmetric interaction i.e. without migration IGpredator is the superior exploitation competitor on the competition patch, but is the inferior one on the predation patch so that IGpredator mainly capture IGprey to maintain [45, 122, 124]. In the predation patch, it is further assumed that IGprey is able to avoid the risk of IGpredator leading to the fact that IGprey drives IGpredator out. Assuming the asymmetric interaction implies the next inequalities hold [105]:

- in the competition patch

$$a_{12}\frac{K_{21}}{K_{11}} > 1 \text{ and } a_{21}\frac{K_{11}}{K_{21}} < 1, \quad (2.2.2)$$

- in the predation patch

$$\frac{d}{eb} > K_{12}. \quad (2.2.3)$$

We investigate the complete model (2.2.1) in the next section.

2.3 Model reduction

Taking advantage of the two time scales, we now use aggregation of variables method in order to derive a reduced model [10, 11, 15, 107]. The first step is to look for existence of a stable and fast equilibrium. The fast equilibrium is the solution of the system (1) while only considering the fast part, i.e. when $\varepsilon = 0$. The fast part corresponds to dispersal, so the fast equilibrium corresponds to the stable distribution corresponding to the dispersal process. We then consider that for the complete model, the system is always at the fast equilibrium, i.e. at any time the distribution of individuals among patches corresponds to the stable distribution. We obtain a model with two equations on which we can perform a mathematical analysis.

2.3.1 Fast equilibrium

Over the fast time scale τ , the total IGprey population ($x(t) = x_1(t) + x_2(t)$) and IGpredator population ($y(t) = y_1(t) + y_2(t)$) are constant. After straightforward calculation, there exists a single fast and stable equilibrium that reads as follows:

- for IGprey:

$$\begin{cases} x_1^* = \frac{m_1}{m_1 + \bar{m}_1} x = \nu_1^* x \\ x_2^* = \frac{\bar{m}_1}{m_1 + \bar{m}_1} x = \nu_2^* x, \end{cases} \quad (2.3.1)$$

- for IGpredator:

$$\begin{cases} y_1^* = \frac{m_2}{m_2 + \bar{m}_2} y = \mu_1^* y \\ y_2^* = \frac{\bar{m}_2}{m_2 + \bar{m}_2} y = \mu_2^* y. \end{cases} \quad (2.3.2)$$

Therefore, the proportions of individuals of IGP in each patch rapidly tend toward to constant values which are proportional to migration rates to the patches.

2.3.2 Aggregated model

Coming back to the complete initial system (2.2.1), we substitute the fast equilibria (2.3.1), (2.3.2) and add the two equations of the local IGprey and IGpredator population densities, leading to the following aggregated system when using the slow time scale t :

$$\begin{cases} \frac{dx}{dt} = x(A - Bx - Cy) \\ \frac{dy}{dt} = y(D - Ey - Fx), \end{cases} \quad (2.3.3)$$

where $A = r_{11}\nu_1^* + r_{12}\nu_2^*$, $B = \frac{r_{11}}{K_{11}}\nu_1^{*2} + \frac{r_{12}}{K_{12}}\nu_2^{*2}$, $C = \frac{r_{11}a_{12}}{K_{11}}\nu_1^*\mu_1^* + b\nu_2^*\mu_2^*$, $D = r_{21}\mu_1^* - d\mu_2^*$, $E = \frac{r_{21}}{K_{21}}\mu_1^{*2}$, $F = \frac{r_{21}a_{21}}{K_{21}}\nu_1^*\mu_1^* - eb\nu_2^*\mu_2^*$.

2.4 Results and discussions

Let's analyse the aggregated model. One can see that system (2.3.3) has four equilibria $P_1(0, 0)$, $P_2(0, D/E)$, $P_3(A/B, 0)$, $P_4((CD - AE)/(CF - BE), (AF - BD)/(CF - BE))$. A full stability analyses of these equilibria is given in Table 2.1.

In summary, the outcome of the dynamics of the aggregated model depends on the signs of $D, F, CD - AE$ and $AF - BD$. These expressions depend on parameters such as the migration parameters (μ and ν), the competition parameters (a_{12} and a_{21}), the predation parameters (b and e), the carrying capacity (K) and so on. Here, we are interested in effects of the migration parameters, the competition parameters and the predation ones. To avoid dealing with complex expressions, we assume the two patches are similar for population growth $r_{11} = r_{12} = r_{21} = r$ and $K_{11} = K_{12} = K_{21} = K$. This yields the following simplified expressions:

$$\begin{aligned} D &= (r + d)\mu_1^* - d, \quad F = \frac{ra_{21}}{K}\nu_1^*\mu_1^* - eb(1 - \nu_1^*)(1 - \mu_1^*), \\ AE &= \frac{r^2}{K}(\mu_1^*)^2, \quad AF = \left(\frac{r^2a_{21}}{K} - ebr\right)\mu_1^*\nu_1^* + ebr\mu_1^* + ebr\nu_1^* - ebr, \\ BD &= \frac{2r(r + d)}{K}\mu_1^*(\nu_1^*)^2 - \frac{2r(r + d)}{K}\mu_1^*\nu_1^* + \frac{r(r + d)}{K}\mu_1^* - \frac{2dr}{K}(\nu_1^*)^2 + \frac{2dr}{K}\nu_1^* - \frac{dr}{K}, \\ CD &= \frac{(r + d)(ra_{12} + bK)}{K}(\mu_1^*)^2\nu_1^* - (r + d)b(\mu_1^*)^2 - \frac{(ra_{12}d + brK + 2bdK)}{K}\mu_1^*\nu_1^* + \\ &\quad (rb + 2bd)\mu_1^* + bd\nu_1^* - bd. \end{aligned}$$

Now we are going to investigate the dynamics in term of the proportion of IGprey on patch 1 (ν_1^*) which is re-denote by X and of the proportion of IGpredator (μ_1^*) which is re-denote by Y . Since the model is a combination of competition and predation models, one could expect that the outcome of the model is also a combination of the outcomes of the two. In fact, the outcome of the model can be all possibilities of the two species, i.e. coexistence and one of the two wins. Figure 2.2a shows an example where the two species coexist. Figure 2.2b illustrates the case where IGpredator wins, while Figure 2.2c illustrates the situation IGprey wins. Figure 2.2d shows the separatrix case where IGpredator or IGprey wins depending on the initial conditions. For these figures, we chose the same values of the following parameters $r_{11} = r_{12} = r_{21} = r_{22} = r = 0.6$, $K_{11} = K_{12} = K_{21} = K = 10$, $a_{12} = 1.5$, $a_{21} = 0.7$, $b = 0.3$, $d = 0.6$ and $e = 0.1$. Then we changed the values of X and Y which correspond to the proportions of IGprey and IGpredator, respectively, on the competition patch. We chose parameters values according to existing literatures. The growth rates are equal to 0.6, the carrying capacities are equal to 10 which are the same magnitude as those found in [64] ($r = 0.44$, $K = 15$) and in [59] ($r = 0.21827$, $K = 13$). The competition coefficients, the predation coefficient and the mortality were chosen the same magnitude as those found in [38, 59, 64, 113] (the competition coefficients are between 0.02 to 3.15, the predation coefficients are between 0.02 to 3 and the mortalities are between 0.055 to 0.52).

Table 2.1: Global outcome of the aggregated model.

D	F	$CD - AE$	$AF - BD$	Equilibria and Stability
+	+	-	+	P_1, P_2 : unstable., P_3 : stable and $P_4 < 0$
+	+	-	-	P_1, P_2, P_3 : unstable, P_4 : stable
+	+	+	+	P_1, P_4 : unstable, P_2, P_3 : stable
+	+	+	-	P_1, P_3 : unstable, P_2 : stable and $P_4 < 0$
+	-	-	-	P_1, P_2, P_3 : unstable, P_4 : stable
+	-	+	-	P_1, P_3 : unstable, P_2 : stable and $P_4 < 0$
-	-	-	-	P_1, P_2, P_3 : unstable, P_4 : stable
-	-	-	+	P_1 : unstable, P_3 : stable, $P_2, P_4 < 0$
-	+	-	+	P_3 : stable, $P_1, P_2, P_4 < 0$

Next we study in detail the dynamics of the aggregated model in term of the migration parameters (i.e. X and Y). Figure 2.3 shows the domains corresponding to the dynamical outcomes of IGpredator and IGprey. We denote by domain I where IGpredator and IGprey coexist. Domain II represents the case where IGpredator wins. Domain III is the domain where IGprey wins. And the domain IV is related to the case where IGpredator or IGprey wins depending on the initial condition. One can see that domain I is related to an interesting result: migration can lead to the coexistence of the two species.

Domain I on top of Figure 2.3 is related to the case in which IGprey individuals are not mainly on the competition patch then they can invade in the predation patch, and IGpredator individuals are almost there on the competition patch where they can invade. On the competition patch, IGprey individuals are able to move very fast to the predation patch so that they can avoid competition with IGpredator individuals. On the predation patch, due to the fast migration IGpredator individuals are able to come to the competition patch rapidly to maintain. Coexistence of the two species is therefore can be possible.

Domain II corresponds to the two situations. The first situation is both species distribute almost on the competition patch where IGpredator can invade. The second situation is IGpredator still distributes mainly on the competition patch, IGprey distributes mainly on the predation patch, but IGpredator distributes well

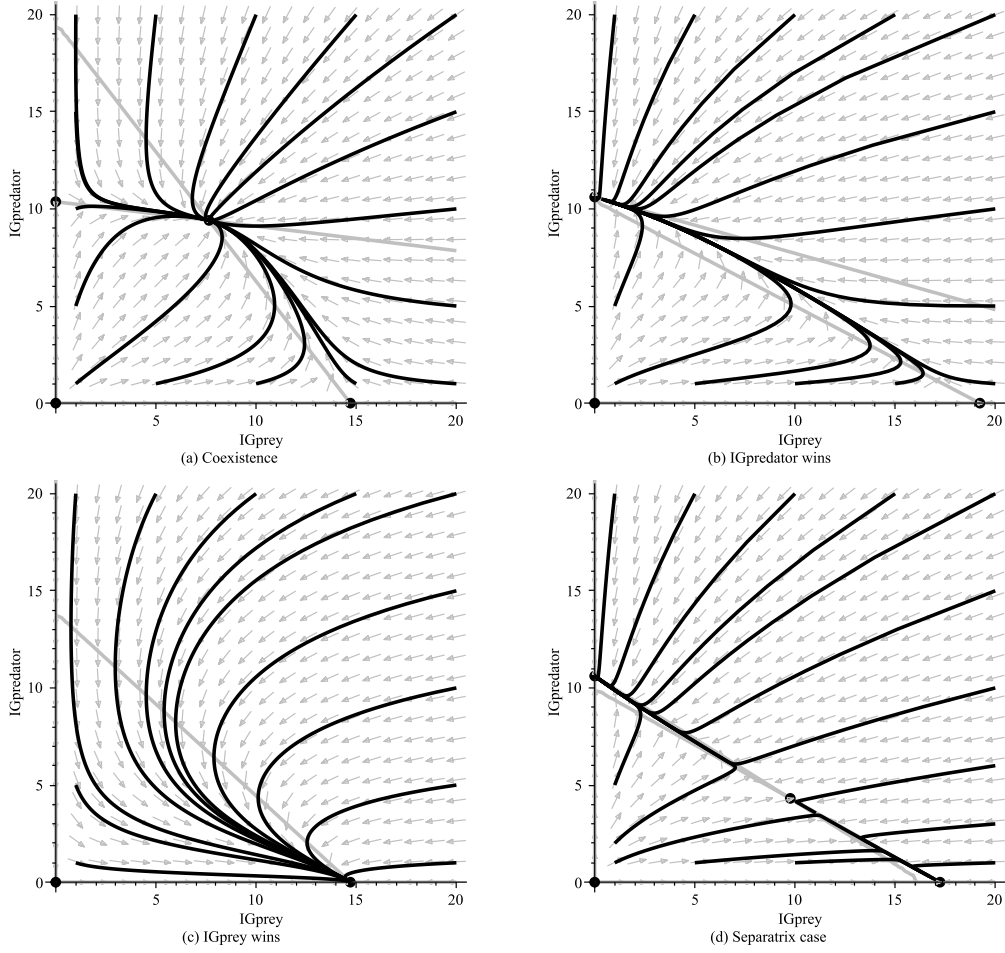


Figure 2.2: Phase portraits of the outcome. Figure 2a is related to coexistence case ($X = 0.2$ and $Y = 0.9$), Figure 2b describes the case where IGpredator wins ($X = 0.4$ and $Y = 0.7$), Figure 2c shows the win of IGprey ($X = 0.8$ and $Y = 0.2$), Figure 2d is the separatrix case ($X = 0.7$ and $Y = 0.7$).

enough on the predation patch in order to gain advantage over IGprey. In both situations, IGpredator wins globally.

Domain III is related to the two cases. The first case is IGpredator individuals are few on the competition patch so that it decreases IGpredation's invasion on this patch. This leads to the fact IGprey is able to invade and to win globally. The second case is IGpredator has comparable distributions on the two patches, but IGprey distributes well enough on the competition patch in order to gain advantage over IGpredator. Therefore, IGprey still wins eventually.

Domain I below of Figure 2.3 links to the the following situation. IGpredator has comparable distributions on the two patches and IGprey distributes mainly on the predation patch. Therefore, the effect of IGprey on IGpredator on the competition patch is not strong yet the abundance of IGprey is better for maintenance of IGpredator on the predation patch. Thus, coexistence can be possible.

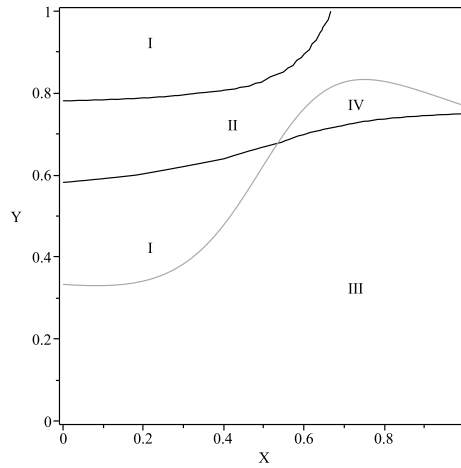


Figure 2.3: Outcomes of the dynamics in term of migration parameters X and Y . The black dash line is about $AE - CD = 0$, the grey dash line is about $AF - BD = 0$. Domain I: coexistence; domain II: IGpredator wins; domain III: IGprey wins; domain IV: separatrix case. Parameters values are chosen as follows: $r_{11} = r_{12} = r_{21} = r_{22} = r = 0.6$, $K_{11} = K_{12} = K_{21} = K = 10$, $a_{12} = 1.5$, $a_{21} = 0.7$, $b = 0.3$, $d = 0.6$ and $e = 0.1$.

Domain IV corresponds to the case where individuals of the two species are mainly on the competition patch. Too many individuals on the competition patch has negative effects on the resource exploitation. Yet a few IGprey individuals on the predation patch not only has negative effects on the maintenance of IGpredator but also decreases its invasion. Globally, this case is disadvantage for both species then species wins depending on the initial condition.

Now, we study effects of competition and predation parameters on the areas of the four domains. Keeping the same values of parameters as in Figure 3, we are going to change the value of one of the three parameters a_{12} , a_{21} and b . According to the conditions (2.2) and (2.3) we have a_{12} is greater than 1, a_{21} is smaller than 1 and b is smaller than $d/(eK) = 0.6$.

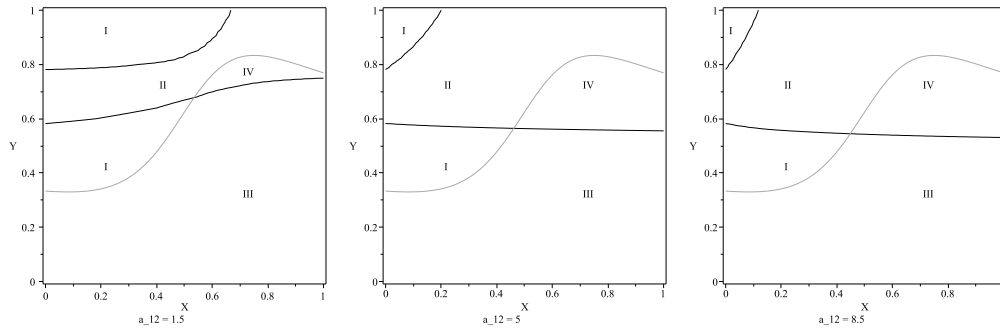
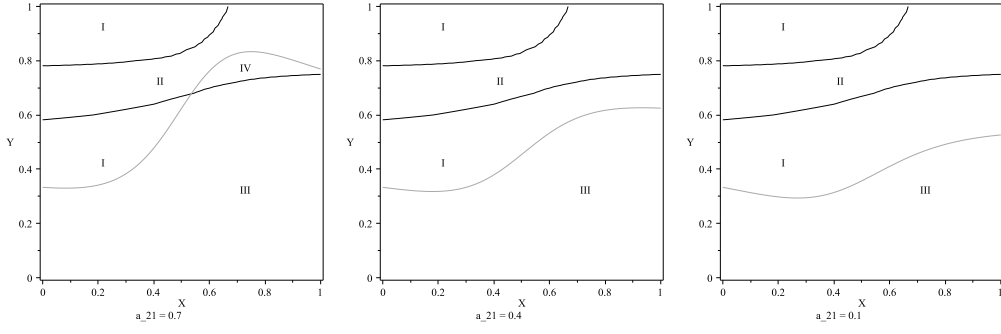
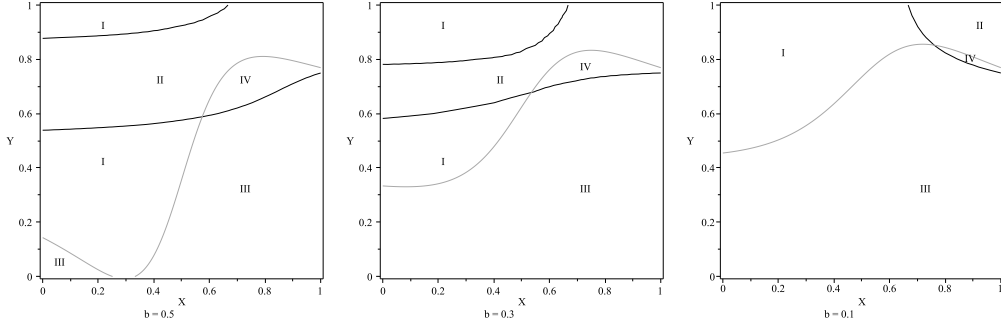


Figure 2.4: The change of the four domains in term of a_{12} .

Figure 2.4 shows three cases from the left to the right where we changed the value

Figure 2.5: The change of the four domains in term of a_{21} .Figure 2.6: The change of the four domains in term of b .

of a_{12} by 1.5, 5 and 8.5, respectively. According to mathematical point of view, the black dash line ($AE - CD = 0$) changes while the grey dash line ($AF - BD = 0$) does not change. According to ecological point of view, increase of a_{12} means that the effect of IGpredator on IGprey on the competition patch increases. Thus, it increases the areas of the domains which are disadvantage for IGprey. In fact, one can observe that part of domain I (both on top and below) now turns into domain II, domain I is therefore gets smaller while domain II gets bigger, and part of domain III now turns into domain IV, domain III is therefore gets smaller while domain IV gets bigger.

Figure 2.5 shows three cases from the left to the right where we changed the value of a_{21} by 0.7, 0.4 and 0.1, respectively. In this case the grey dash line changes while the black dash line does not change. We decrease the value of a_{21} meaning that the effect of IGprey on IGpredator on the competition patch decreases too. So, it decreases the areas of the domains which are disadvantage for IGpredator. One can observe that domain IV turns into domain II, part of domain III turns into domain I below. Therefore, domain III gets smaller, domain IV disappears, domain II and domain I below get bigger.

Figure 2.6 shows three cases from the left to the right where we changed the value of b by 0.5, 0.3 and 0.1, respectively. In this case, both the black dash and grey dash lines change. For instance, when the value of b increases from 0.3 to 0.5 it implies that IGpredator's predation ability increases. So, it increases the areas of

the domains which are advantage for IGpredator and it decreases the areas of the domains which are not harmful for IGPrey. One can observe that part of domain I turns into domain II, part of domain III turns into domain I below and domain IV. Thus domain II, domain I below and domain IV get bigger and domain I on top and domain III get smaller. Now, when the value of b decreases from 0.3 to 0.1 it follows that IGpredator's predation ability decreases. Therefore, it decreases the areas of the domains which are advantage for IGpredator and it increases the areas of the domains which are not harmful for IGPrey. In fact, one can observe that domain I below and part of domain IV turn into domain III, part of domain II turns into domain I. Hence domain I and domain III get bigger, domain II and domain IV get smaller.

2.5 Conclusion and perspectives

We have presented an IGP model in a two-patch environment: the interaction on a given patch is pure competition and that on the other patch is predation. We focus in particular on an asymmetric interaction i.e. without migration IGpredator is the superior exploitation competitor on the competition patch, but is the inferior one on the predation patch so that IGPredator mainly capture IGprey to maintain. We concentrated on the case where the predation is weak leading to the fact that IGprey wins on the predation patch.

The model is a coupling a classical competition model on a given patch and a classical predation model on the other patch. The two patches are connected by a fast migration of individuals. This assumption allows us to obtain the aggregated model which can be investigated analytically. As a first result, we showed that the IGP dynamics can be either competition or predation depending on the parameters. Figure 2.2 showed that all outcomes of the interaction of the two species can be achieved: coexistence, IGpredator wins, IGprey wins, species wins depending on the initial condition. Here we focus on migration, competition and predation parameters. When we fix competition and predation parameters, outcome of the dynamics depends migration parameters. We obtain four domains corresponding to the outcomes (Figure 2.3). When we respectively changed competition and predation parameters, the four domains changed (Figure 2.4, 2.5 and 2.6).

In our model, IGprey and IGpredator cannot coexist locally in the sense that each species is able to out-compete the other without migration: IGpredator wins on the competition patch and IGprey wins on the predation patch. Coexistence of the two species can be achieved under certain conditions. When each species individuals are almost there on the patch where they can invade, coexistence can be possible. The two species can also coexist when IGpredator has comparable distributions on the two patches and IGprey distributes mainly on the predation patch. In this situation, IGprey is abundant on the patch where it can invade and it survives globally. IGpredator individuals can capture more IGprey individuals on the predation patch, yet they compete with few IGprey individuals on the competition

patch, hence IGpredator can also survive globally.

The current contribution is the first attempt to investigate the effects of heterogeneous environment on IGP dynamics. In this study, we do not take into account density-dependent migration, different predation types such as Holling type II, III and so on. It would be also interesting to consider these factors in the near future.

Chapter 3

Effect of small versus large clusters of fish school on the yield of a purse-seine small pelagic fishery including a marine protected area

3.1 Introduction

This chapter shows paper [110]. There was an increasing interest in modelling the dynamics of a fishery, we refer to review and classical contributions dealing with mathematical approaches [41, 85, 132, 133], and more ecological ones [32, 56, 97, 147]. Spatio-temporal distribution is a major factor affecting fish catchability, particularly for small pelagic fish [8]. Small pelagic fish species are the most exploited fish species at the world level and play a major role in world food security [136]. However, these populations are threatened by both climate change [31, 54] and over-fishing [119]. Thus, there is a need of research to feed future management plans for these species.

Here, we present a mathematical model of a fishery targeting a small pelagic fish population distributed over two sites, a MPA and a fishing area where the fish population can be captured by purse-seine fishing boats. Following the literature [29, 116] we assume that small pelagic fish can either be distributed in few large clusters of fish school (hereafter referred as "cluster") or in a greater number of smaller clusters [116]. There is evidence that large clusters are generally more easily located by fishing boats than smaller ones [30]. Industrial fishing fleets use electronic devices such as sonar to detect school and the efficiency is better for large school [28] which may occur more often in large clusters [116]. Fishermen of artisanal fleets can even simply detect fish school by visual observation when the school is close to the surface (upper part of the water column). Thus, once fishermen detected a school that belongs to a large cluster, they access easily the other fish schools that belong to this cluster. Furthermore, purse-seine fisheries generally operate in collaborative

fleets of several boats and join their efforts on large clusters. As a consequence, fish in large clusters are more exposed to fishing pressure due to increased accessibility.

The aim of the present model is to investigate the effects of fish clustering on the total catch of a small pelagic purse seine fishery. What are the effects of large or small clusters on the global dynamics of the fishery? Is there a proportion of small and large clusters which is optimal in terms of total catch on the long term for a given fishery and fishing effort?

The complete model is a set of 5 coupled ordinary differential equations (ODEs) with four variables representing fish populations divided into large or small clusters and located in MPA or in fishing area, and one variable representing a single fishing effort in the fishing area whatever the cluster size. We further assume that there are three time scales: fish can migrate from MPA to the fishing area at a very fast time scale, fish can change state from small to large clusters at a fast time scale and fish growth and catch occur at a slow time scale.

To our knowledge, aggregation methods were not used to aggregate a system involving three time scales. This contribution thus shows an example of aggregation of variables in a three level system. This aggregation of a three level system requires a two-step aggregation, aggregating firstly from very fast to fast dynamics and secondly from fast to slow dynamics. Here, we simply proceed to aggregation in order to derive the slow aggregated model. We numerically show that the aggregation method is valid as soon as there exists (for the present case) an order of magnitude between two consecutive time scales (fast/very fast) or (slow/fast). Under these conditions, numerical simulations show that the dynamics of the complete and the aggregated models are very similar, i.e. the trajectories of both systems starting at the same initial conditions remain close to each other.

This chapter is organized as follows. Section 3.2 presents the complete fishery model. Section 3.3 and 3.4 present the aggregation method in order to derive a global model at the slow time scale with two consecutive steps. Section 3.5 studies the effects of exploited fish population structuration in small vs. large clusters on the total catch of the fishery. The chapter ends with a discussion according to our theoretical results on the yield of a given fishery and opens some perspectives.

3.2 Complete Model

We consider a population of fish that is harvested. The model takes into account fish densities and the fishing effort. The model is a two sites model: a Marine Protected Area or MPA (index M) where fishing is prohibited and a Fishing area (index F) where the fish population is harvested. We assume that fish can migrate from MPA to fishing area F and inversely. Furthermore, fish school can belong to Small clusters (index S) or to Large clusters (index L). We assume that fish can change state from S to L and inversely. Therefore, fish school can leave large clusters to form small clusters and inversely (see figure 3.1). Fish population grows logistically with a total carrying capacity K with a fraction h in MPA and $(1 - h)$

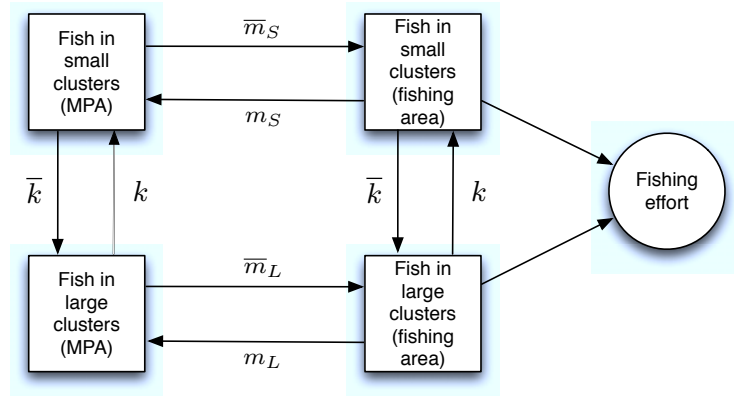


Figure 3.1: Diagram of the model used in this study showing the interactions between aggregative dynamics (small to large clusters and vis versa) and the migration between fishing and marine protected areas (MPA). See table 3.1 for parameters description.

in the fishing area. Fish are captured in the fishing area according to a Schaefer function [128]. As a consequence, there are 4 fish sub-populations in the model:

- n_{SM} : density of fish in small clusters in MPA;
- n_{LM} : density of fish in large clusters in MPA;
- n_{SF} : density of fish in small clusters in fishing area;
- n_{LF} : density of fish in large clusters in fishing area.

There is a single fishing effort in the fishing area noted E . The model reads as follows:

$$\left\{ \begin{array}{l} \frac{dn_{SM}}{d\tau} = (m_S n_{SF} - \bar{m}_S n_{SM}) + \varepsilon(k n_{LM} - \bar{k} n_{SM}) \\ \quad \quad \quad + \varepsilon \mu \left(r n_{SM} \left(1 - \frac{n_{SM} + n_{LM}}{hK} \right) \right) \\ \frac{dn_{LM}}{d\tau} = (m_L n_{LF} - \bar{m}_L n_{LM}) + \varepsilon(\bar{k} n_{SM} - k n_{LM}) \\ \quad \quad \quad + \varepsilon \mu \left(r n_{LM} \left(1 - \frac{n_{SM} + n_{LM}}{hK} \right) \right) \\ \frac{dn_{SF}}{d\tau} = (\bar{m}_S n_{SM} - m_S n_{SF}) + \varepsilon(k n_{LF} - \bar{k} n_{SF}) \\ \quad \quad \quad + \varepsilon \mu \left(r n_{SF} \left(1 - \frac{n_{SF} + n_{LF}}{(1-h)K} \right) \right) - \varepsilon \mu q_S n_{SF} E \\ \frac{dn_{LF}}{d\tau} = (\bar{m}_L n_{LM} - m_L n_{LF}) + \varepsilon(\bar{k} n_{SF} - k n_{LF}) \\ \quad \quad \quad + \varepsilon \mu \left(r n_{LF} \left(1 - \frac{n_{SF} + n_{LF}}{(1-h)K} \right) \right) - \varepsilon \mu q_L n_{LF} E \\ \frac{dE}{d\tau} = \varepsilon \mu (-cE + p q_S n_{SF} E + p q_L n_{LF} E), \end{array} \right. \quad (3.2.1)$$

Table 3.1: Description of all parameters for the complete model.

K	total carrying capacity of MPA and fishing area
h	proportion of MPA, $0 < h < 1$
k	rate of change of fish state from large clusters to small clusters
\bar{k}	rate of change of fish state from small clusters to large clusters
m_L	rate of migration from fishing area to MPA for fish in large clusters
\bar{m}_L	rate of migration from MPA to fishing area for fish in large clusters
m_S	rate of migration from fishing area to MPA for fish in small clusters
\bar{m}_S	rate of migration from MPA to fishing area for fish in small clusters
r	growth rate of fish
q_S	catchability for fish in small clusters
q_L	catchability for fish in large clusters
c	average cost per unit of fishing effort
p	constant market price

where all parameters are defined in Table 3.1.

We suppose that $q_S < q_L$, i.e. fishermen catch much better fish in large clusters than in small ones. We further assume that there exist three time scales:

- Migration (MPA/fishing area) is a very fast process;
- State change (Small clusters/Large clusters) is a fast process;
- Catch and growth are slow processes.

Therefore, we assume that there exist two dimensionless parameters $\varepsilon \ll 1$ and $\mu \ll 1$ being of the same order. Consequently, the model takes into account three time scales:

- a very fast time: τ ;
- a fast time: $t = \varepsilon\tau$;
- a slow time: $T = \mu t = \mu\varepsilon\tau$;

leading to the next relation for any time dependent variable X :

$$\frac{dX}{d\tau} = \varepsilon \frac{dX}{dt} = \mu\varepsilon \frac{dX}{dT}.$$

The MPA is assumed to be ~ 10 km diameter, roughly the maximum size for a cluster [116], so that time scale for fish movement from MPA to fishing area (and inversely) is approximately a day. The model could be applied to any exploited aggregative small pelagic fish which forms large clusters that remain coherent at least ~ 10 days. In West Africa, one could think about the *Sardinella aurita* population

as an example. We assume in this work that the small clusters work as a refuge, i.e. their catchability is inferior to large clusters' one, considering the case study of purse-seine fishery because of reduced accessibility as explained in the introduction. Finally, to be consistent with the mechanisms and behaviours associated to the three times scales, theses must correspond to ~ 1 day (very fast), ~ 10 days (fast) and ~ 100 days (slow). This respects the empirical condition for aggregation methods to work, i.e. one order of magnitude between the time scales as we show in the next section.

3.3 Building the aggregated model

Now, we shall take advantage of the three time scales to build a reduced model governing the total fish density and the total fishing effort. Aggregation methods were introduced in ecology by Iwasa et al [73, 74]. Here, we use time scale separation methods based on the central manifold theory and we refer to the following articles for aggregation methods [10, 11, 14]. Usually, the complete system involves only two time scales. Under this condition, the aggregation is realized by calculating the fast equilibrium and the aggregated model is obtained by substituting the fast equilibrium into the complete model.

In our present case, three time scales are considered. As a consequence, the aggregation is going to require two steps. In a first step, we shall look for the existence of a very fast equilibrium and we shall substitute it into the complete model. This will lead to an "intermediate" model at the fast time scale. The second and last step will consist in looking for the existence of a fast equilibrium whose substitution in the intermediate model will lead to the aggregated and final slow model.

3.3.1 First step of aggregation: very fast fish movements

Let us set $\varepsilon = \mu = 0$ leading to the very fast model that describes the patch change from MPA to fishing area and inversely:

$$\begin{cases} \frac{dn_{SM}}{d\tau} = m_S n_{SF} - \bar{m}_S n_{SM} \\ \frac{dn_{LM}}{d\tau} = m_L n_{LF} - \bar{m}_L n_{LM} \\ \frac{dn_{SF}}{d\tau} = \bar{m}_S n_{SM} - m_S n_{SF} \\ \frac{dn_{LF}}{d\tau} = \bar{m}_L n_{LM} - m_L n_{LF} \\ \frac{dE}{d\tau} = 0. \end{cases}$$

At the very fast time scale, the sub-populations small and large clusters are constant, i.e. the next variables are first integrals:

$$n_S = n_{SM} + n_{SF},$$

$$n_L = n_{LM} + n_{LF}.$$

A simple calculation leads to the next very fast equilibrium for small clusters:

$$n_{SM}^* = \frac{m_S}{\bar{m}_S + m_S} n_S = \nu_{SM}^* n_S,$$

$$n_{SF}^* = \frac{\bar{m}_S}{\bar{m}_S + m_S} n_S = \nu_{SF}^* n_S,$$

where ν_{SF}^* is the proportion of small clusters in the fishing area and ν_{SM}^* in MPA. Similarly for fish in large clusters we get the very fast equilibrium as follows:

$$n_{LM}^* = \frac{m_L}{\bar{m}_L + m_L} n_L = \nu_{LM}^* n_L,$$

$$n_{LF}^* = \frac{\bar{m}_L}{\bar{m}_L + m_L} n_L = \nu_{LF}^* n_L,$$

where ν_{LF}^* is the proportion of large fish clusters in the fishing area and ν_{LM}^* in MPA. After substitution of this very fast equilibrium into the complete model, we get the "intermediate" model, i.e. the fast model (or first aggregated model) which reads:

$$\begin{cases} \frac{dn_S}{dt} = (kn_L - \bar{k}n_S) + \mu \left(r\nu_{SM}^* n_S \left(1 - \frac{\nu_{SM}^* n_S + \nu_{LM}^* n_L}{hK} \right) \right. \\ \quad \left. + \mu \left(r\nu_{SF}^* n_S \left(1 - \frac{\nu_{SF}^* n_S + \nu_{LF}^* n_L}{(1-h)K} \right) \right) - \mu q_S \nu_{SF}^* n_S E \right) \\ \frac{dn_L}{dt} = (\bar{k}n_S - kn_L) + \mu \left(r\nu_{LM}^* n_L \left(1 - \frac{\nu_{SM}^* n_S + \nu_{LM}^* n_L}{hK} \right) \right. \\ \quad \left. + \mu \left(r\nu_{LF}^* n_L \left(1 - \frac{\nu_{SF}^* n_S + \nu_{LF}^* n_L}{(1-h)K} \right) \right) - \mu q_L \nu_{LF}^* n_L E \right) \\ \frac{dE}{dt} = \mu(-cE + pq_S \nu_{SF}^* n_S E + pq_L \nu_{LF}^* n_L E). \end{cases} \quad (3.3.1)$$

3.3.2 Second step of aggregation: fast changes in clusters size

Let set $\mu = 0$ in the previous first aggregated model leading to the next fast model:

$$\begin{cases} \frac{dn_S}{dt} = kn_L - \bar{k}n_S \\ \frac{dn_L}{dt} = \bar{k}n_S - kn_L \\ \frac{dE}{dt} = 0. \end{cases}$$

At the fast time scale, the total fish population is constant: $n = n_S + n_L$. A simple calculation leads to the next fast equilibrium for small clusters and large clusters:

$$n_S^* = \frac{k}{\bar{k} + k} n = \nu_S^* n,$$

$$n_L^* = \frac{\bar{k}}{\bar{k} + k} n = \nu_L^* n.$$

Substitution of the fast equilibrium into the "intermediate" model leads to the final aggregated model (at the slow time scale) governing the total fish density and the fishing effort:

$$\left\{ \begin{array}{l} \frac{dn}{dT} = r\nu_{SM}^*\nu_S^*n \left(1 - \frac{(\nu_{SM}^*\nu_S^* + \nu_{LM}^*\nu_L^*)n}{hK} \right) \\ \quad + r\nu_{SF}^*\nu_S^*n \left(1 - \frac{(\nu_{SF}^*\nu_S^* + \nu_{LF}^*\nu_L^*)n}{(1-h)K} \right) \\ \quad + r\nu_{LM}^*\nu_L^*n \left(1 - \frac{(\nu_{SM}^*\nu_S^* + \nu_{LM}^*\nu_L^*)n}{hK} \right) \\ \quad + r\nu_{LF}^*\nu_L^*n \left(1 - \frac{(\nu_{SF}^*\nu_S^* + \nu_{LF}^*\nu_L^*)n}{(1-h)K} \right) \\ \quad - q_S\nu_{SF}^*\nu_S^*nE - q_L\nu_{LF}^*\nu_L^*nE \\ \frac{dE}{dT} = (-c + pq_S\nu_{SF}^*\nu_S^*n + pq_L\nu_{LF}^*\nu_L^*n)E. \end{array} \right. \quad (3.3.2)$$

By setting

$$\begin{aligned} \Phi &= q_S\nu_{SF}^*\nu_S^* + q_L\nu_{LF}^*\nu_L^*, \\ \frac{1}{\kappa} &= \frac{1}{K} \left(\frac{(\nu_{SF}^*\nu_S^* + \nu_{LF}^*\nu_L^* + h - 1)^2}{h(1-h)} + 1 \right), \end{aligned}$$

model (3.3.2) can be written as:

$$\left\{ \begin{array}{l} \frac{dn}{dT} = rn \left(1 - \frac{n}{\kappa} \right) - \Phi n E \\ \frac{dE}{dT} = (-c + p\Phi n)E. \end{array} \right. \quad (3.3.3)$$

Model (3.3.3) is classic Lotka-Volterra predator-prey model with logistics growth for prey (see [22, 86]). We see that it has two trivial equilibria: $(0, 0)$, $(\kappa, 0)$ and a non-trivial equilibrium point $(n^*, E^*) = (\frac{c}{p\Phi}, \frac{r}{\Phi}(1 - \frac{c}{p\Phi\kappa}))$. The global dynamics of model (3.3.3) depend on the sign of (n^*, E^*) :

- If $p\Phi\kappa > c$, (n^*, E^*) is globally asymptotically stable;
- If $p\Phi\kappa < c$, $(\kappa, 0)$ is globally asymptotically stable.

Figure 3.2 shows comparison of the trajectories of complete and aggregated models in the same case and initial conditions for different values of the small parameters, (a) $\varepsilon = \mu = 1$, (b) $\varepsilon = 1$ and $\mu = 0.1$, (c) $\varepsilon = 0.1$ and $\mu = 1$, (d) $\varepsilon = \mu = 0.1$. Grey trajectory corresponds to the complete model and the black one the aggregated model. The solutions of both models (3.2.1) and (3.3.3) have the same dynamical behaviour. However, to have trajectories close enough of each other we need to chose ε and μ at least smaller than 0.1 as shown on figure 3.2(d). Figure 3.3 shows a similar result in the case of fleet effort extinction. This means that aggregation methods in this three level system can be successfully used when there exists at least an order of magnitude between two consecutive time scales. In the case of smaller values such as $\varepsilon = \mu = 0.01$, the approximation would be improved such that trajectories of aggregated and complete models would become extremely close and would appear confounded.

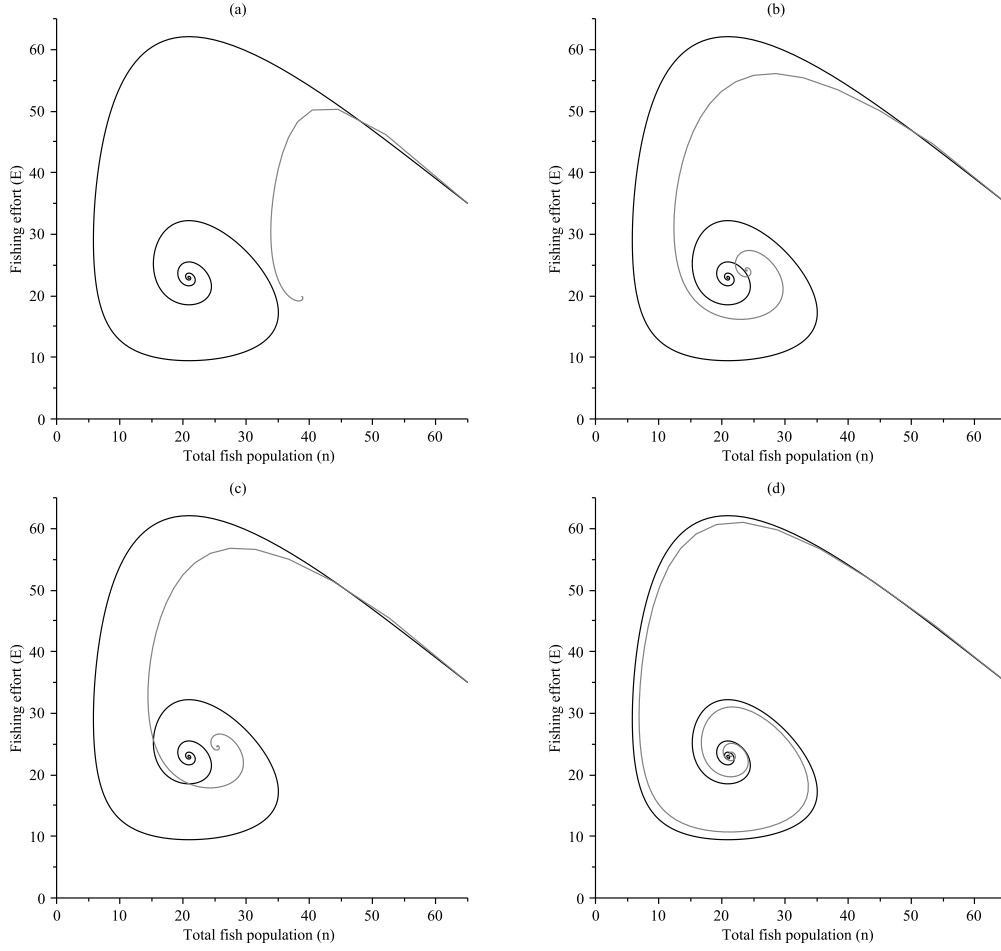


Figure 3.2: Orbit of complete (grey) and aggregated (black) models in case of a sustainable fishery. $E^* > 0$ when: (a) $\varepsilon = \mu = 1$, (b) $\varepsilon = 1, \mu = 0.1$, (c) $\varepsilon = 0.1, \mu = 1$, (d) $\varepsilon = \mu = 0.1$ and $m_S = 0.8, \bar{m}_S = 0.3, m_L = 0.6, \bar{m}_L = 0.5, k = 0.7, \bar{k} = 0.4, r = 0.9, h = 0.4, K = 100, c = 0.6, p = 1, q_S = 0.07, q_L = 0.1$, with initial values $n_{SM}(0) = 20, n_{LM}(0) = 15, n_{SF}(0) = 10, n_{LF}(0) = 20, E(0) = 35$.

3.4 Comparison with one-step aggregation

It would have been possible to decide to perform only a one-step aggregation. The first possibility is to assume that $\varepsilon = 0$ in order to study the very fast dynamics, and then not assuming that $\mu = 0$. This corresponds to the first step of the previous aggregation and leads to a three equation system, which is more difficult to analyse than the previous aggregated model. The other possibility is to assume that $\mu = 0$ in order to study the fast dynamics, without assuming at any moment that $\varepsilon = 0$.

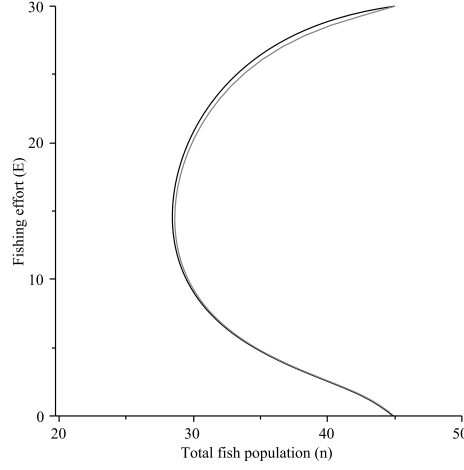


Figure 3.3: Orbit of complete (grey) and aggregated (black) models in case of a stable fishery free equilibrium. $E^* < 0$ when $\varepsilon = \mu = 0.1, m_S = 0.4, \bar{m}_S = 0.7, m_L = 0.5, \bar{m}_L = 0.5, k = 0.3, \bar{k} = 0.6, r = 0.7, h = 0.3, K = 50, c = 0.9, p = 1, q_S = 0.02, q_L = 0.04$, with initial values $n_{SM}(0) = 15, n_{LM}(0) = 10, n_{SF}(0) = 12, n_{LF}(0) = 8, E(0) = 30$.

Fast dynamics is then governed by the following set of equations:

$$\begin{cases} \frac{dn_{SM}}{d\tau} = (m_S n_{SF} - \bar{m}_S n_{SM}) + \varepsilon(k n_{LM} - \bar{k} n_{SM}) \\ \frac{dn_{LM}}{d\tau} = (m_L n_{LF} - \bar{m}_L n_{LM}) + \varepsilon(\bar{k} n_{SM} - k n_{LM}) \\ \frac{dn_{SF}}{d\tau} = (\bar{m}_S n_{SM} - m_S n_{SF}) + \varepsilon(k n_{LF} - \bar{k} n_{SF}) \\ \frac{dn_{LF}}{d\tau} = (\bar{m}_L n_{LM} - m_L n_{LF}) + \varepsilon(\bar{k} n_{SF} - k n_{LF}) \\ \frac{dE}{d\tau} = 0. \end{cases} \quad (3.4.1)$$

Solving $dn_{SM}/d\tau = dn_{LM}/d\tau = dn_{SF}/d\tau = dn_{LF}/d\tau = 0$ is equivalent to solving a linear system. We obtain:

$$\begin{aligned} \nu_{SM}^*(\varepsilon) &= \frac{k (\varepsilon (m_S k + m_L \bar{k}) + m_S (m_L + \bar{m}_L))}{(k + \bar{k}) (\varepsilon (m_S k + \bar{m}_S k + m_L \bar{k} + \bar{m}_L \bar{k}) + (m_S + \bar{m}_S) (m_L + \bar{m}_L))}, \\ \nu_{LM}^*(\varepsilon) &= \frac{\bar{k} (\varepsilon (m_S k + m_L \bar{k}) + m_L (m_S + \bar{m}_S))}{(k + \bar{k}) (\varepsilon (m_S k + \bar{m}_S k + m_L \bar{k} + \bar{m}_L \bar{k}) + (m_S + \bar{m}_S) (m_L + \bar{m}_L))}, \\ \nu_{SF}^*(\varepsilon) &= \frac{k (\varepsilon (\bar{m}_S k + \bar{m}_L \bar{k}) + \bar{m}_S (m_L + \bar{m}_L))}{(k + \bar{k}) (\varepsilon (m_S k + \bar{m}_S k + m_L \bar{k} + \bar{m}_L \bar{k}) + (m_S + \bar{m}_S) (m_L + \bar{m}_L))}, \\ \nu_{LF}^*(\varepsilon) &= \frac{\bar{k} (\varepsilon (\bar{m}_S k + \bar{m}_L \bar{k}) + \bar{m}_L (m_S + \bar{m}_S))}{(k + \bar{k}) (\varepsilon (m_S k + \bar{m}_S k + m_L \bar{k} + \bar{m}_L \bar{k}) + (m_S + \bar{m}_S) (m_L + \bar{m}_L))}. \end{aligned}$$

It is easy to verify that:

$$\begin{aligned}\lim_{\varepsilon \rightarrow 0} \nu_{SM}^*(\varepsilon) &= \nu_{SM}^* \nu_S^* = \frac{m_S k}{(m_S + \bar{m}_S)(k + \bar{k})}, \\ \lim_{\varepsilon \rightarrow 0} \nu_{LM}^*(\varepsilon) &= \nu_{LM}^* \nu_L^* = \frac{m_L \bar{k}}{(m_L + \bar{m}_L)(k + \bar{k})}, \\ \lim_{\varepsilon \rightarrow 0} \nu_{SF}^*(\varepsilon) &= \nu_{SF}^* \nu_S^* = \frac{\bar{m}_S k}{(m_S + \bar{m}_S)(k + \bar{k})}, \\ \lim_{\varepsilon \rightarrow 0} \nu_{LF}^*(\varepsilon) &= \nu_{LF}^* \nu_L^* = \frac{\bar{m}_L \bar{k}}{(m_L + \bar{m}_L)(k + \bar{k})}.\end{aligned}$$

The system obtained after a two-step aggregation appears as an approximation for $\varepsilon = 0$ of the one-step aggregation. The dynamics obtained is a slightly better approximation of the complete dynamics than the one obtained with the two-step aggregation method. Indeed, substituting the frequencies at the fast equilibrium which are solutions of equations (3.4.1) would lead to another one-step aggregated model that could be developed as a Taylor expansion with respect to ε . The zero order term of this Taylor expansion would exactly correspond to the aggregated model (3.3.3) obtained by the two-step method but, with the advantage that the first order term would give a correction term of the order of ε leading to a better approximation of the complete model. However, determining the frequencies at fast equilibrium is more difficult than with the two-step aggregation methods: it requires solving a four-dimension system of equations in order to determine the fast equilibrium (first four equations of system (3.4.1)). The two-step method requires solving more (three) systems of equations, but with a lower number of equations (only two equations).

To summarize, two aggregation methods have been proposed:

- The two-step method leads to an aggregated model with less approximation but in most cases, it could be easier to handle it as it can be switched into several systems of equations, very fast and fast.
- The one-step method allows to calculate some correction terms leading to a better approximation but, we need to deal with a single system of equations to get the fast equilibrium. The later system may be more difficult to handle analytically.

3.5 Harvest Optimization

Now, we shall study the effect of clusters size distribution on the total catch of the fishery at equilibrium. The catch per unit of time at equilibrium of the slow aggregated model reads as follows:

$$Y = \Phi n^* E^* = \frac{rc}{p\Phi} \left(1 - \frac{c}{p\Phi\kappa}\right). \quad (3.5.1)$$

We shall study the effect of the proportion of fish in small clusters on the total catch. Thus, let us write the catch Y as a function of the proportion of fish in small clusters at fast equilibrium, i.e. function of ν_S^* . For simplicity we denote by X this proportion. According to that notation, we obtain:

$$Y = \frac{A_1 X^2 + A_2 X + A_3}{(A_4 X + A_5)^2}, \quad 0 < X < 1, \quad (3.5.2)$$

in which:

$$\begin{aligned} A_1 &= -c^2 r (\nu_{SF}^* - \nu_{LF}^*)^2, \\ A_2 &= c r p K h (1 - h) (q_S \nu_{SF}^* - q_L \nu_{LF}^*) + 2c^2 r (1 - h - \nu_{LF}^*) (\nu_{SF}^* - \nu_{LF}^*), \\ A_3 &= c r (1 - h) (p K h q_L \nu_{LF}^* + 2c \nu_{LF}^{*2} - c) - c^2 r \nu_{LF}^{*2}, \\ A_4 &= p (q_S \nu_{SF}^* - q_L \nu_{LF}^*) \sqrt{h(1 - h)K}, \\ A_5 &= p q_L \nu_{LF}^* \sqrt{h(1 - h)K}. \end{aligned} \quad (3.5.3)$$

We will find out condition for the existence of a local maximum of Y with respect to $X \in (0, 1)$. We see that equation $Y'(X) = 0$ has unique solution:

$$X^* = -\frac{A_2 A_5 - 2A_4 A_3}{2A_1 A_5 - A_2 A_4}. \quad (3.5.4)$$

The second order derivative of Y at X^* is:

$$\frac{d^2 Y}{dX^2}(X^*) = \frac{(2A_1 A_5 - A_2 A_4)^4}{8(-A_4 A_2 A_5 + A_4^2 A_3 + A_1 A_5^2)^3}. \quad (3.5.5)$$

Hence, all conditions for the existence of local maximum of Y with $X \in (0, 1)$ can reduce as follows:

$$0 < -\frac{A_2 A_5 - 2A_4 A_3}{2A_1 A_5 - A_2 A_4} < 1, \quad (3.5.6)$$

$$-A_4 A_2 A_5 + A_4^2 A_3 + A_1 A_5^2 < 0. \quad (3.5.7)$$

Under condition (3.5.6) and (3.5.7), we obtain the maximum of Y :

$$Y^* = \frac{4A_3 A_1 - A_2^2}{4(-A_4 A_2 A_5 + A_4^2 A_3 + A_1 A_5^2)}. \quad (3.5.8)$$

In our model, fish that form small clusters act as a refuge. A fishery can be considered as a predator-prey system, the prey being the fish and the predator, the fishing fleet. Such classical prey-predator (Lotka-Volterra and Holling type II) as well as inter-specific competition models with a refuge have already been investigated [47, 62, 83, 109].

Figure 3.4 shows that there exists a maximum of the total catch at equilibrium with respect to the proportion of small clusters. Indeed, since we consider small pelagic fish species and purse-seine fisheries, the catchability is inferior for small clusters than for large one, and captured fish mainly belong to large clusters.

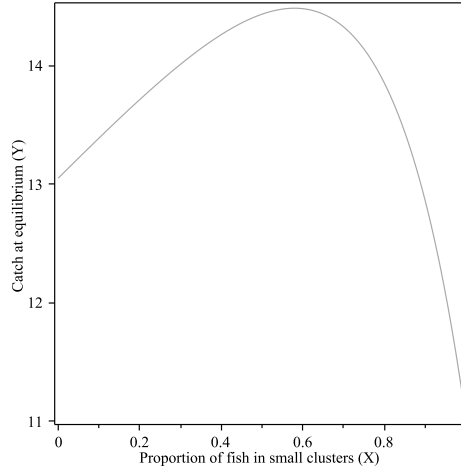


Figure 3.4: Total catch as a function of the proportion of small clusters showing a maximum corresponding to maximum sustainable yield. The coefficients are $m_S = 0.8$, $\bar{m}_S = 0.2$, $m_L = 0.7$, $\bar{m}_L = 0.3$, $r = 0.9$, $h = 0.4$, $K = 100$, $c = 0.6$, $p = 1$, $q_S = 0.07$, $q_L = 0.1$.

Starting from a fish population organized only in large clusters, increasing the proportion of small clusters firstly reduce the overall population catchability, since we assumed a lower catchability for small clusters. Such catchability reduction can be seen as a refuge effect that benefit population growth, and once the equilibrium is reached it allows to increase the total catch (because the population density is higher). Globally, this is favorable to the growth of the fish population and it allows to increase the total catch at equilibrium.

Besides, if a too large proportion of fish is structured in small clusters, the reduction in catchability is not anymore compensated by the growth of biomass due to the refuge effect described before, and as a result the yield decrease. Consequently, there is a proportion of small fish clusters in between that maximizes the total catch at equilibrium as shown on figure 3.4.

3.6 Discussion and perspectives

Our model has shown that for small pelagic fish, there exists a maximum of the total catch with respect to the size distribution of the clusters. Another aspect regarding optimal spatial distribution of a fishing fleet in a patchy fishery was also investigated in [100].

As a result of our model, over-fishing would progressively give advantage to fish populations that are able to change rapidly from small clusters to large clusters and inversely. Being part of small clusters works as a kind of refuge for fish because the catch is less, considering that large clusters can be more easily detected by fishermen and thus exploited than small ones.

Our model does consider only two cluster sizes, large and small. In a further contribution, it would be interesting to consider a more continuous size spectrum for clusters. Does small pelagic fish species display different levels of exposure to over fishing following their specific clustering behavior?

The theoretical results obtained in this work, if they are validated on a particular fishery, could be translated in near real time management policy. Indeed, even if we do not yet understand well the determinism of small pelagic fish aggregative dynamics [29], we know that it is possible to control the harvesting process in near real time (e.g. as it is the case in Peru; Pers. Comm. Arnaud Bertrand). Nevertheless observation methodologies of cluster size have been already developed, particularly using acoustics devices [92], in continuous monitoring [30] and near real time [27]. Thus, a near real time management could be encouraged, on the basis of this work, to control harvesting in order to produce an optimal value for ν_S^* . Such supervision should allow adaptive management measures, according to the variation of biotic and abiotic factors, to target the maximum sustainable yield of a fishery. However this require to improve our understanding of the effect of the environment on the aggregative dynamics of exploited small pelagic fish as well as the processes affecting their biomass variability and fluctuation.

The present chapter allowed us to extend aggregation of variables methods to a three level dynamical system. Aggregation in a two level system is rather usual. Here, we extended the method for a system involving three time scales and we present an aggregation method with double steps. In the present work, we simply proceed to aggregation and show by numerical simulations of a particular case that the method works quite well when there is at least an order of magnitude between two consecutive time scales.

In the future, it would be useful to present aggregation methods of three (or more) level systems in a general context and to show that the center manifold theory can be extended to the case of a system of ODEs with several time scales. The two-step methods offer the same benefits than well-known *divide-and-conquer* algorithms which aim at dividing a problem into several sub-problems that are simpler to solve. This method could prove to be of particular interest for larger dimension problems, or for problems for which fast equilibria have to be determined from non-linear systems of equations.

Chapter 4

Dynamics of species in a model with two predators and one prey

4.1 Introduction

Paper [140] is presented in this chapter. The dynamical relationship between predators and prey has been studied by several authors for a long time. In those researches, to represent the average number of prey killed per individual predator per unit of time, a functional, called functional response, was introduced. One functional response can depend on only the prey's density or both the prey's and the predator's densities. However, some biologists have argued that in many situation, especially when predators have to search for food, the functional response should depend on both prey's and predator's densities [5, 6, 50, 77, 78, 130]. One of the most popular functional responses is the fractional one as in the following prey-predator model. It is called Beddington-DeAngelis functional response.

$$\begin{cases} x_1' = x_1(a_1 - b_1x_1) - \frac{c_1x_1x_2}{\alpha + \beta x_1 + \gamma x_2}, \\ x_2' = -a_2x_2 + \frac{c_2x_1x_2}{\alpha + \beta x_1 + \gamma x_2}. \end{cases}$$

In this model, $x_i(t)$ represents the population density of species X_i at time t ($i \geq 1$); X_1 is the prey and X_2 is the predator. At time t , $a_1(t)$ is the intrinsic growth rate of X_1 and $a_i(t)$ is the death rate of X_2 ; $b_1(t)$ measures the inhibiting effect of environment on X_1 . This model was originally proposed by Beddington [23] and DeAngelis et al. [48], independently. After the appearance of these two investigations, there are many other ones for analogous systems with diffusion in a constant environment [35, 36, 37, 43, 70, 71]. However, the constant environment is rarely the case in real life. Most natural environments are physically highly variable, i.e., the coefficients in those models should depend on time [46, 53, 139, 150]. In order to continue studying such models, in this chapter, we consider a predator-prey model of one prey and two

predators with Beddington-DeAngelis functional responses

$$\begin{cases} x'_1 = x_1 [a_1(t) - b_1(t)x_1] - \frac{c_2(t)x_1x_2}{\alpha(t)+\beta(t)x_1+\gamma(t)x_2} - \frac{c_3(t)x_1x_3}{\alpha(t)+\beta(t)x_1+\gamma(t)x_3}, \\ x'_2 = x_2 \left[-a_2(t) + \frac{d_2(t)x_1}{\alpha(t)+\beta(t)x_1+\gamma(t)x_2} - b_2(t)x_3 \right], \\ x'_3 = x_3 \left[-a_3(t) + \frac{d_3(t)x_1}{\alpha(t)+\beta(t)x_1+\gamma(t)x_3} - b_3(t)x_2 \right]. \end{cases} \quad (4.1.1)$$

Here $x_i(t)$ represents the population density of species X_i at time t ($i \geq 1$), X_1 is the prey and X_2, X_3 are the predators. Two predators share one prey and it is assumed that there are two types of competition between two predators. The first type is direct interference where individuals of each predator species act with aggression against individuals of the other predator species. In our model, this type of competition is described by the coefficients $b_2(t)$ and $b_3(t)$. The second type of competition is interference competition that occurs during hunting because predators spend time interacting with each other rather than seeking prey. Here we assume that there is no competition of that type between individuals of the two different predator species. Therefore, the Beddington-DeAngelis functional responses are of the form $\frac{d_i(t)x_1}{\alpha(t)+\beta(t)x_1+\gamma(t)x_i}$ ($i = 2, 3$). We use the same coefficients α, β, γ in the functional responses of both predators, since it is assumed that both predators take the same time to handle a prey once they encounter it and that individuals of each predator species interfere with each other when hunting by exactly the same amount in both species. This assumption is somewhat restrictive from the biological viewpoint, but it could be removed without greatly changing the analysis of system (4.1.1).

Throughout this chapter, it is assumed that the functions $a_i(t), b_{ij}(t), c_i(t), d_i(t), \alpha(t), \beta(t), \gamma(t)$ ($1 \leq i, j \leq 3$) are continuous on \mathbb{R} and bounded above and below by some positive constants.

This chapter is organized as follows. Section 4.2 provides some definitions and notation. In Section 4.3, we state some results on invariant set, the permanence and extinction of system (4.1.1). Then, the asymptotic stability of solution is proved by using a Liapunov function. In Section 4.4, we continue using other Liapunov functions and the continuation theorem in coincidence degree theory to show the existence and global stability of a positive periodic solution. The final section 4.5 illustrates the behavior of system (4.1.1) by some computational results and gives our conclusion.

4.2 Definitions and notation

In this section we introduce some basic definitions and facts which will be used throughout this chapter. Let $\mathbb{R}_+^3 = \{(x_1, x_2, x_3) \in \mathbb{R}^3 \mid x_i > 0 \ (i \geq 1)\}$. Denote by $x(t) = (x_1(t), x_2(t), x_3(t))$ the solution of system (4.1.1) with initial condition $x^0 = (x_1^0, x_2^0, x_3^0) = (x_1(t_0), x_2(t_0), x_3(t_0))$, $t_0 \geq 0$. For biological reasons, throughout this chapter, we only consider the solutions $x(t)$ with positive initial values, i.e., $x^0 \in \mathbb{R}_+^3$. Let $g(t)$ be a continuous function, for a brevity, instead of writing $g(t)$ we

write g . If g is bounded on \mathbb{R} , we denote

$$g^u = \sup_{t \in \mathbb{R}} g(t), \quad g^l = \inf_{t \in \mathbb{R}} g(t),$$

and $\hat{g} = \frac{1}{\omega} \int_0^\omega g(t) dt$, if g is a periodic function with period ω . The global existence and uniqueness of solution of system (4.1.1) are guaranteed by the properties of the map defined by the right hand of system (4.1.1)[19]. We have the following lemma

Lemma 4.1. *Both the non-negative and positive cones of \mathbb{R}^3 are positively invariant for (4.1.1).*

Proof. The solution $x(t)$ of (4.1.1) with initial value x^0 satisfies

$$\begin{cases} x_1 = x_1^0 \exp \left\{ \int_{t_0}^t \left[a_1 - b_1 x_1 - \frac{c_2 x_2}{\alpha + \beta x_1 + \gamma x_2} - \frac{c_3 x_3}{\alpha + \beta x_1 + \gamma x_3} \right] du \right\}, \\ x_2 = x_2^0 \exp \left\{ \int_{t_0}^t \left[-a_2 + \frac{d_2 x_1}{\alpha + \beta x_1 + \gamma x_2} - b_2 x_3 \right] du \right\}, \\ x_3 = x_3^0 \exp \left\{ \int_{t_0}^t \left[-a_3 + \frac{d_3 x_1}{\alpha + \beta x_1 + \gamma x_3} - b_3 x_2 \right] du \right\}. \end{cases}$$

The conclusion follows immediately for all $t \in [t_0, \infty)$. The proof is complete. \square

Definition 4.2. System (4.1.1) is said to be permanent if there exist some positive δ_j ($j = 1, 2$) such that

$$\delta_1 \leq \liminf_{t \rightarrow \infty} x_i(t) \leq \limsup_{t \rightarrow \infty} x_i(t) \leq \delta_2 \quad (i \geq 1)$$

for all solutions of (4.1.1).

Definition 4.3. A set $A \subset \mathbb{R}_+^3$ is called an ultimately bounded region of system (4.1.1) if for any solution $x(t)$ of (4.1.1) with positive initial values, there exists $T_1 > 0$ such that $x(t) \in A$ for all $t \geq t_0 + T_1$.

Definition 4.4. A bounded non-negative solution $x^*(t)$ of (4.1.1) is said to be globally asymptotically stable (or globally attractive) if any other solution $x(t)$ of (4.1.1) with positive initial values satisfies $\lim_{t \rightarrow \infty} \sum_{i=1}^3 |x_i(t) - x_i^*(t)| = 0$.

Remark 4.5. It is easy to see that if a solution of (4.1.1) is globally asymptotically stable, then so are all solutions. In this case, system (4.1.1) is also said to be globally asymptotically stable.

4.3 The model with general coefficients

Let $\epsilon \geq 0$ be sufficient small. Put

$$\begin{aligned} M_1^\epsilon &= \frac{a_1^u}{b_1^l} + \epsilon, \quad M_i^\epsilon = \frac{d_i^u M_1^\epsilon - a_i^l \alpha^l}{a_i^l \gamma^l}, \\ m_1^\epsilon &= \frac{a_1^l \gamma^l - c_2^u - c_3^u}{b_1^u \gamma^l} - \epsilon, \\ m_i^\epsilon &= \frac{d_i^l m_1^\epsilon - (a_i^u + b_i^u M_j^\epsilon)(\beta^u m_1^\epsilon + \alpha^u)}{(a_i^u + b_i^u M_j^\epsilon) \gamma^u} \quad (i, j \geq 2, i \neq j) \end{aligned} \tag{4.3.1}$$

then $M_i^\epsilon > m_i^\epsilon$ ($i \geq 1$). We will show that $\max\{m_i^0, 0\}$ ($i \geq 1$) are the lower bounds for the limiting bounds of species X_i as time t tends to infinity. This is obvious when $m_i^0 \leq 0$. Therefore, it is assumed that $m_i^0 > 0$.

Hypothesis 4.6. $m_i^0 > 0$ ($i \geq 1$).

Theorem 4.7. *Under Hypothesis 4.6, for any sufficient small $\epsilon > 0$ such that $m_i^\epsilon > 0$ ($i \geq 1$), a set Γ_ϵ defined by $\Gamma_\epsilon = \{(x_1, x_2, x_3) \in \mathbb{R}^3 \mid m_i^\epsilon < x_i < M_i^\epsilon \text{ } (i \geq 1)\}$ is positively invariant with respect to system (4.1.1).*

Proof. Through out this proof, we use the facts that the solution to the equation

$$X'(t) = A(t, X)X(t)[B - X(t)] \quad (B \neq 0)$$

is given by

$$X(t) = \frac{BX^0 \exp \left\{ \int_{t_0}^t BA(s, X(s))ds \right\}}{X^0 \left[\exp \left\{ \int_{t_0}^t BA(s, X(s))ds \right\} - 1 \right] + B},$$

where $t_0 \geq 0$ and $X^0 = X(t_0)$. Consider the solution of system (4.1.1) with an initial value $x^0 \in \Gamma_\epsilon$. From Lemma 4.1 and from the first equation of (4.1.1), we have

$$\begin{aligned} x_1'(t) &\leq x_1(t)[a_1(t) - b_1(t)x_1(t)] \\ &\leq x_1(t)[a_1^u - b_1^l x_1(t)] \\ &= b_1^l x_1(t)(M_1^0 - x_1). \end{aligned}$$

Using the comparison theorem gives

$$\begin{aligned} x_1(t) &\leq \frac{x_1^0 M_1^0 \exp\{a_1^u(t - t_0)\}}{x_1^0 [\exp\{a_1^u(t - t_0)\} - 1] + M_1^0} \\ &\leq \frac{x_1^0 M_1^\epsilon \exp\{a_1^u(t - t_0)\}}{x_1^0 [\exp\{a_1^u(t - t_0)\} - 1] + M_1^\epsilon} \\ &< M_1^\epsilon, \quad t \geq t_0. \end{aligned} \tag{4.3.2}$$

It follows from the third equation of (4.1.1) and from (4.3.2) that

$$\begin{aligned} x_2' &\leq -a_2^l x_2 + \frac{d_2^u x_1 x_2}{\alpha^l + \beta^l x_1 + \gamma^l x_2} \\ &\leq -a_2^l x_2 + \frac{d_2^u M_1^\epsilon x_2}{\alpha^l + \gamma^l x_2} \\ &= \frac{x_2 [(d_2^u M_1^\epsilon - a_2^l \alpha^l) - a_2^l \gamma^l x_2]}{\alpha^l + \gamma^l x_2} \\ &= \frac{a_2^l \gamma^l}{\alpha^l + \gamma^l x_2} x_2 (M_2^\epsilon - x_2). \end{aligned}$$

Putting

$$C_2(t) = \frac{a_2^l \gamma^l}{\alpha^l + \gamma^l x_2(t)}, \tag{4.3.3}$$

and using the comparison theorem again yield

$$x_2(t) \leq \frac{M_2^\epsilon x_2^0 \exp \left\{ M_2^\epsilon \int_{t_0}^t C_2(s) ds \right\}}{x_2^0 \left[\exp \left\{ M_2^\epsilon \int_{t_0}^t C_2(s) ds \right\} - 1 \right] + M_2^\epsilon} < M_2^\epsilon, \quad t \geq t_0. \quad (4.3.4)$$

Similarly, $x_3(t) < M_3^\epsilon$ for every $t \geq t_0$.

Now by the first equation of (4.1.1), it implies that

$$x_1'(t) \geq x_1 \left(a_1^l - \frac{c_2^u + c_3^u}{\gamma^l} - b_1^u x_1 \right) = b_1^u x_1 (m_1^0 - x_1).$$

Since $x_1^0 > m_1^\epsilon$, by the comparison theorem, we obtain

$$x_1(t) \geq \frac{x_1^0 m_1^0 \exp \{ b_1^u m_1^0 (t - t_0) \}}{x_1^0 [\exp \{ b_1^u m_1^0 (t - t_0) \} - 1] + m_1^0} > m_1^\epsilon \quad \text{for all } t \geq t_0.$$

Similarly, for $i, j \geq 2$ ($i \neq j$),

$$\begin{aligned} x_i' &= -a_i x_i + \frac{d_i x_1 x_i}{\alpha + \beta x_1 + \gamma x_i} - b_i x_i x_j \\ &\geq -(a_i^u + b_i^u M_j^\epsilon) x_i + \frac{d_i^l m_1^\epsilon x_i}{\alpha^u + \beta^u m_1^\epsilon + \gamma^u x_i} \\ &= \frac{[d_i^l m_1^\epsilon - (a_i^u + b_i^u M_j^\epsilon)(\beta^u m_1^\epsilon + \alpha^u)] x_i - (a_i^u + b_i^u M_j^\epsilon) \gamma^u x_i^2}{\alpha^u + \beta^u m_1^\epsilon + \gamma^u x_i} \\ &= \frac{(a_i^u + b_i^u M_j^\epsilon) \gamma^u}{\alpha^u + \beta^u m_1^\epsilon + \gamma^u x_i} x_i (m_i^\epsilon - x_i), \end{aligned}$$

from which follows that $x_i(t) > m_i^\epsilon$ for all $t \geq t_0$. We complete the proof. \square

In the next theorem, the permanence of system (4.1.1) is shown. A treatment called practical persistence to prove the permanence of models and its application to various types of models can be seen in [34, 35, 42].

Theorem 4.8. *Under Hypothesis 4.6, for any sufficient small $\epsilon > 0$ such that $m_i^\epsilon > 0$,*

$$m_i^\epsilon \leq \liminf_{t \rightarrow \infty} x_i(t) \leq \limsup_{t \rightarrow \infty} x_i(t) \leq M_i^\epsilon \quad (i \geq 1).$$

Consequently, system (4.1.1) is permanent.

Proof. According to the proof of Theorem 4.7 we have

$$x_1(t) \leq \frac{x_1^0 M_1^0 \exp \{ a_1^u (t - t_0) \}}{x_1^0 [\exp \{ a_1^u (t - t_0) \} - 1] + M_1^0}.$$

Thus, $\limsup_{t \rightarrow \infty} x_1(t) \leq M_1^0$, i.e., there exists $t_1 \geq t_0$ such that $x_1(t) < M_1^\epsilon$ for all $t \geq t_1$. By the same arguments of making (4.3.4), it follows that

$$x_2(t) \leq \frac{M_2^\epsilon x_2^1 \exp \left\{ M_2^\epsilon \int_{t_1}^t C_2(s) ds \right\}}{x_2^1 \left[\exp \left\{ M_2^\epsilon \int_{t_1}^t C_2(s) ds \right\} - 1 \right] + M_2^\epsilon}, \quad (4.3.5)$$

from which implies $0 < x_2(t) \leq \max\{M_2^\epsilon, x_2^1\}$ for all $t \geq t_1$, where $x_2^1 = x_2(t_1)$. Then from (4.3.3), $\inf_{t \geq t_1} C_2(s) > 0$. By using (4.3.5), we have $\limsup_{t \rightarrow \infty} x_2(t) \leq M_2^\epsilon$. Similarly, $\limsup_{t \rightarrow \infty} x_3(t) \leq M_3^\epsilon$ and $\liminf_{t \rightarrow \infty} x_i(t) \geq m_i^\epsilon$ ($i \geq 1$). The permanence follows from Definition 4.2. The proof is complete. \square

Theorem 4.9. *Let $i \in \{2, 3\}$. If $M_i^0 < 0$ then $\lim_{t \rightarrow \infty} x_i(t) = 0$, i.e., the i^{th} -predator goes to extinction.*

Proof. It follows from $M_i^0 < 0$ that $M_i^\epsilon < 0$ with a sufficiently small ϵ . Similarly to the proof of Theorem 4.7 we have

$$x_i'(t) \leq \frac{a_i^l \gamma^l}{\alpha^l + \gamma^l x_i} x_i (M_i^\epsilon - x_i) < 0. \quad (4.3.6)$$

Thus, there exists $C \geq 0$ such that $\lim_{t \rightarrow \infty} x_i(t) = C$ and $C \leq x_i(t) \leq x_i^0$ for all $t \geq t_0$. If $C > 0$ then from (4.3.6), there exists $\mu > 0$ such that $x_i'(t) < -\mu$ for all $t \geq t_0$. We therefore have $x_i(t) < -\mu(t - t_0) + x_i^0$ and then $\lim_{t \rightarrow \infty} x_i(t) = -\infty$, which contradicts $x_i(t) > 0$ for all $t \geq t_0$. Hence, $\lim_{t \rightarrow \infty} x_i(t) = 0$. \square

In order to consider the global asymptotic stability of system (4.1.1), we need the following result called Barbalat's lemma.

Lemma 4.10. *(see [20].) Let h be a real number and f be a non-negative function defined on $[h, +\infty)$ such that f is integrable and uniformly continuous on $[h, +\infty)$. Then $\lim_{t \rightarrow \infty} f(t) = 0$.*

Theorem 4.11. *Suppose that Hypothesis 4.6 holds and let $\epsilon > 0$ be sufficient small such that $m_i^\epsilon > 0$ ($i \geq 1$). Let x^* be a solution of system (4.1.1) satisfying*

$$\begin{aligned} \limsup_{t \rightarrow \infty} \left\{ -b_1 + \frac{\beta c_2 M_2^\epsilon + d_2(\alpha + \gamma M_2^\epsilon)}{u_2(m_1^\epsilon, M_2^\epsilon)} + \frac{\beta c_3 M_3^\epsilon + d_3(\alpha + \gamma M_3^\epsilon)}{u_3(m_1^\epsilon, M_3^\epsilon)} \right\} &< 0, \\ \limsup_{t \rightarrow \infty} \left\{ b_j + \frac{c_i(\alpha + \beta M_1^\epsilon)}{u_i(M_1^\epsilon, m_i^\epsilon)} - \frac{d_i \gamma m_1^\epsilon}{u_i(m_1^\epsilon, M_i^\epsilon)} \right\} &< 0, \end{aligned} \quad (4.3.7)$$

where $u_i(a, b) = (\alpha + \beta x_1^* + \gamma x_i^*)(\alpha + \beta a + \gamma b)$ ($i, j \geq 2, i \neq j$). Then x^* is globally asymptotically stable.

Proof. Let x be other solution of (4.1.1). From Corollary 4.8, Γ_ϵ is an ultimately bounded region of (4.1.1). Then there exists $T_1 > 0$ such that $x, x^* \in \Gamma_\epsilon$ for all $t \geq t_0 + T_1$. Consider a Liapunov function defined by $V(t) = \sum_{i=1}^3 |\ln x_i - \ln x_i^*|$, $t \geq t_0$. A direct calculation of the right derivative $D^+V(t)$ of $V(t)$ along the solution of

(4.1.1) gives

$$\begin{aligned}
D^+V(t) &= \sum_{i=1}^3 \operatorname{sgn}(x_i - x_i^*) \left(\frac{x_i'}{x_i} - \frac{x_i^{*'}}{x_i^*} \right) \\
&= \operatorname{sgn}(x_1 - x_1^*) \left[-c_2 \left(\frac{x_2}{\alpha + \beta x_1 + \gamma x_2} - \frac{x_2^*}{\alpha + \beta x_1^* + \gamma x_2^*} \right) \right. \\
&\quad \left. - c_3 \left(\frac{x_3}{\alpha + \beta x_1 + \gamma x_3} - \frac{x_3^*}{\alpha + \beta x_1^* + \gamma x_3^*} \right) - b_1(x_1 - x_1^*) \right] \\
&\quad + d_2 \operatorname{sgn}(x_2 - x_2^*) \left[\frac{x_1}{\alpha + \beta x_1 + \gamma x_2} - \frac{x_1^*}{\alpha + \beta x_1^* + \gamma x_2^*} - \frac{b_2}{d_2}(x_3 - x_3^*) \right] \\
&\quad + d_3 \operatorname{sgn}(x_3 - x_3^*) \left[\frac{x_1}{\alpha + \beta x_1 + \gamma x_3} - \frac{x_1^*}{\alpha + \beta x_1^* + \gamma x_3^*} - \frac{b_3}{d_3}(x_2 - x_2^*) \right] \\
&\leq -b_1|x_1 - x_1^*| - c_2 \operatorname{sgn}(x_1 - x_1^*) \frac{\alpha(x_2 - x_2^*) + \beta(x_1^*x_2 - x_1x_2^*)}{u_2(x_1, x_2)} \\
&\quad - c_3 \operatorname{sgn}(x_1 - x_1^*) \frac{\alpha(x_3 - x_3^*) + \beta(x_1^*x_3 - x_1x_3^*)}{u_3(x_1, x_3)} \\
&\quad + d_2 \operatorname{sgn}(x_2 - x_2^*) \frac{\alpha(x_1 - x_1^*) + \gamma(x_1x_2^* - x_2x_1^*)}{u_2(x_1, x_2)} + b_2|x_3 - x_3^*| \\
&\quad + d_3 \operatorname{sgn}(x_3 - x_3^*) \frac{\alpha(x_1 - x_1^*) + \gamma(x_1x_3^* - x_3x_1^*)}{u_3(x_1, x_3)} + b_3|x_2 - x_2^*|.
\end{aligned}$$

It follows from $x, x^* \in \Gamma_\epsilon$ for $t \geq t_0 + T_1$ and $x_1x_i^* - x_1^*x_i = x_1(x_i^* - x_i) + x_i(x_1 - x_1^*)$ ($i = 2, 3$) that

$$\begin{aligned}
D^+V(t) &\leq -b_1|x_1 - x_1^*| - c_2 \operatorname{sgn}(x_1 - x_1^*) \frac{(\alpha + \beta x_1)(x_2 - x_2^*) - \beta x_2(x_1 - x_1^*)}{u_2(x_1, x_2)} \\
&\quad - c_3 \operatorname{sgn}(x_1 - x_1^*) \frac{(\alpha + \beta x_1)(x_3 - x_3^*) - \beta x_3(x_1 - x_1^*)}{u_3(x_1, x_3)} \\
&\quad + d_2 \operatorname{sgn}(x_2 - x_2^*) \frac{(\alpha + \gamma x_2)(x_1 - x_1^*) - \gamma x_1(x_2 - x_2^*)}{u_2(x_1, x_2)} + b_2|x_3 - x_3^*| \\
&\quad + d_3 \operatorname{sgn}(x_3 - x_3^*) \frac{(\alpha + \gamma x_3)(x_1 - x_1^*) - \gamma x_1(x_3 - x_3^*)}{u_2(x_1, x_3)} + b_3|x_2 - x_2^*| \\
&\leq \left[-b_1 + \frac{\beta c_2 M_2^\epsilon + d_2(\alpha + \gamma M_2^\epsilon)}{u_2(m_1^\epsilon, M_2^\epsilon)} + \frac{\beta c_3 M_3^\epsilon + d_3(\alpha + \gamma M_3^\epsilon)}{u_3(m_1^\epsilon, M_3^\epsilon)} \right] |x_1 - x_1^*| \\
&\quad + \left[b_3 + \frac{c_2(\alpha + \beta M_1^\epsilon)}{u_2(M_1^\epsilon, m_2^\epsilon)} - \frac{d_2 \gamma m_1^\epsilon}{u_2(m_1^\epsilon, M_2^\epsilon)} \right] |x_2 - x_2^*| \\
&\quad + \left[b_2 + \frac{c_3(\alpha + \beta M_1^\epsilon)}{u_3(M_1^\epsilon, m_3^\epsilon)} - \frac{d_3 \gamma m_1^\epsilon}{u_3(m_1^\epsilon, M_3^\epsilon)} \right] |x_3 - x_3^*| \quad \text{for } t \geq t_0 + T_1.
\end{aligned} \tag{4.3.8}$$

Combining (4.3.7) and (4.3.8) gives the existence of a positive number $\mu > 0$ and of

$T_2 \geq t_0 + T_1$ such that

$$D^+V(t) \leq -\mu \sum_{i=1}^3 |x_i - x_i^*| \quad \text{for every } t \geq T_2. \quad (4.3.9)$$

Integrating both sides of (4.3.9) from T_2 to t yields

$$V(t) + \mu \int_{T_2}^t \left(\sum_{i=1}^3 |x_i - x_i^*| \right) ds \leq V(T_2) < \infty \quad \text{for every } t \geq T_2.$$

Then $\int_{T_2}^t \left(\sum_{i=1}^3 |x_i - x_i^*| \right) ds \leq \mu^{-1} V(T_2) < \infty$ for every $t \geq T_2$. Hence, $\sum_{i=1}^3 |x_i - x_i^*| \in L^1([T_2, \infty))$.

On the other hand, it follows from $x, x^* \in \Gamma_\epsilon$ for all $t \geq t_0 + T_1$ and from equations of (4.1.1) that the derivatives of $x_i(t), x_i^*(t) (i \geq 1)$ are bounded on $[T_2, \infty)$. As a consequence $\sum_{i=1}^3 |x_i - x_i^*|$ is uniformly continuous on $[T_2, \infty)$. By Lemma 4.10 we have $\lim_{t \rightarrow \infty} \sum_{i=1}^3 |x_i - x_i^*| = 0$, which completes the proof. \square

4.4 The model with periodic coefficients

In this section, we assume that the coefficients in system (4.1.1) are ω -periodic in t and bounded above and below by some positive constants. We study the existence and stability of a periodic solution of this system. To do this, we will employ the alternative approach to establish some criteria in terms of the average of the related functions over an interval of the common period. That is continuation theorem in coincidence degree theory, which has been successfully used to establish criteria for the existence of positive periodic solutions of some mathematical models of predator-prey type, we refer the reader to [89, 90, 91, 126]. To this end, we shall summarize in the following a few concepts and results from [57] that will be basic for this section.

Let \mathbb{X} and \mathbb{Y} be two Banach spaces, let $L : \text{Dom} L \subset \mathbb{X} \rightarrow \mathbb{Y}$ be a linear mapping, and let $N : \mathbb{X} \rightarrow \mathbb{Y}$ be a continuous mapping. The mapping L will be called a Fredholm mapping of index zero if the following conditions hold

- (i) $\text{Im} L$ is closed.
- (ii) $\dim \text{Ker} L = \text{codim Im} L < \infty$.

If L is a Fredholm mapping of index zero and there exist continuous projections $P : \mathbb{X} \rightarrow \mathbb{X}$ and $Q : \mathbb{Y} \rightarrow \mathbb{Y}$ such that $\text{Im} P = \text{Ker} L, \text{Im} L = \text{Ker} Q = \text{Im}(I - Q)$, it follows that

$$L_p = L|_{\text{Dom} L \cap \text{Ker} P} : (I - P)\mathbb{X} \rightarrow \text{Im} L$$

is invertible. We denote by K_p the inverse of that map. If Ω is an open bounded subset of \mathbb{X} , the mapping N will be called L -compact on $\bar{\Omega}$ if the mapping $QN : \bar{\Omega} \rightarrow \mathbb{Y}$ is continuous and bounded, and $K_p(I - Q)N : \bar{\Omega} \rightarrow \mathbb{X}$ is compact, i.e., it is

continuous and $K_p(I - Q)N(\bar{\Omega})$ is relatively compact. Since $\text{Im}Q$ is isomorphic to $\text{Ker}L$, there exists an isomorphism $J: \text{Im}Q \rightarrow \text{Ker}L$. The following continuation theorem is from [57].

Lemma 4.12. (*Continuation theorem*) *Let \mathbb{X} and \mathbb{Y} be two Banach spaces and L a Fredholm mapping of index zero. Assume that $N: \bar{\Omega} \rightarrow \mathbb{Y}$ is L -compact on $\bar{\Omega}$ with Ω is open and bounded in \mathbb{X} . Furthermore, assume that*

(a) *for each $\lambda \in (0, 1)$, $x \in \partial\Omega \cap \text{Dom}L$, $Lx \neq \lambda Nx$;*

(b) *for each $x \in \partial\Omega \cap \text{Ker}L$, $QNx \neq 0$;*

(c) $\deg\{QNx, \Omega \cap \text{Ker}L, 0\} \neq 0$;

then the operator equation $Lx = Nx$ has at least one solution in $\text{Dom}L \cap \bar{\Omega}$.

We now put

$$\begin{aligned} L_{11} &= \ln \frac{\hat{a}_1}{\hat{b}_1}, H_{11} = \ln \frac{\hat{a}_1}{\hat{b}_1} + 2\hat{a}_1\omega, \\ L_{12} &= \ln \left\{ \hat{a}_1 - \widehat{\left(\frac{c_2 + c_3}{\gamma}\right)} \right\}, H_{12} = L_{12} - 2\hat{a}_1\omega, \\ L_{i1} &= \ln \frac{\hat{a}_1(\hat{d}_i - \hat{a}_i\beta^l) \exp\{2\hat{a}_1\omega\} - \hat{a}_i\hat{b}_1\alpha^l}{\hat{a}_i\hat{b}_1\gamma^l}, \\ H_{i1} &= 2\widehat{\left(\frac{d_i}{\beta}\right)}\omega + L_{i1}, \\ L_{i2} &= \ln \frac{d_i \exp\{H_{12}\} - (\alpha^u + \beta^u \exp\{H_{12}\})(\hat{a}_i + \hat{b}_i \exp\{H_{j1}\})}{\gamma^u(\hat{a}_i + \hat{b}_i \exp\{H_{j1}\})}, \\ H_{i2} &= L_{i2} - 2\widehat{\left(\frac{d_i}{\beta}\right)}\omega \quad (i, j \geq 2, i \neq j). \end{aligned}$$

The convention here is that $\ln x = -\infty$ if $x \leq 0$. In the next theorem, a sufficient condition for existence of an ω -periodic solution of (4.1.1) is presented.

Theorem 4.13. *If $L_{i2} > -\infty$ ($i \geq 1$) then system (4.1.1) has at least one positive ω -periodic solution.*

Proof. Put $x_i(t) = \exp\{u_i(t)\}$ ($i \geq 1$), then system (4.1.1) becomes

$$\begin{cases} u'_1 = a_1 - b_1 \exp\{u_1\} - \frac{c_2 \exp\{u_2\}}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_2\}} - \frac{c_3 \exp\{u_3\}}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_3\}}, \\ u'_2 = -a_2 + \frac{d_2 \exp\{u_1\}}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_2\}} - b_2 \exp\{u_3\}, \\ u'_3 = -a_3 + \frac{d_3 \exp\{u_1\}}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_3\}} - b_3 \exp\{u_2\}. \end{cases} \quad (4.4.1)$$

Let $\mathbb{X} = \mathbb{Y} = \{u = (u_1, u_2, u_3)^T \in \mathbb{C}^1(\mathbb{R}, \mathbb{R}^3) \mid u_i(t) = u_i(t + \omega) \ (i \geq 1)\}$ with $\|u\| = \sum_{i=1}^3 \max_{t \in [0, T]} |u_i(t)|$, $u \in \mathbb{X}$. Then \mathbb{X}, \mathbb{Y} are both Banach spaces with the above norm $\|\cdot\|$. Let

$$\begin{aligned} N \begin{bmatrix} u_1 \\ u_2 \\ u_3 \end{bmatrix} &= \begin{bmatrix} N_1(t) \\ N_2(t) \\ N_3(t) \end{bmatrix} \\ &= \begin{bmatrix} a_1 - b_1 \exp\{u_1\} - \frac{c_2 \exp\{u_2\}}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_2\}} - \frac{c_3 \exp\{u_3\}}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_3\}} \\ -a_2 + \frac{d_2 \exp\{u_1\}}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_2\}} - b_2 \exp\{u_3\} \\ -a_3 + \frac{d_3 \exp\{u_1\}}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_3\}} - b_3 \exp\{u_2\} \end{bmatrix}, \\ L \begin{bmatrix} u_1 \\ u_2 \\ u_3 \end{bmatrix} &= \begin{bmatrix} u'_1 \\ u'_2 \\ u'_3 \end{bmatrix}, P \begin{bmatrix} u_1 \\ u_2 \\ u_3 \end{bmatrix} = Q \begin{bmatrix} u_1 \\ u_2 \\ u_3 \end{bmatrix} = \begin{bmatrix} \frac{1}{\omega} \int_0^\omega u_1(t) dt \\ \frac{1}{\omega} \int_0^\omega u_2(t) dt \\ \frac{1}{\omega} \int_0^\omega u_3(t) dt \end{bmatrix}, \begin{bmatrix} u_1 \\ u_2 \\ u_3 \end{bmatrix} \in \mathbb{X}. \end{aligned}$$

Then $\text{Ker} L = \{u \in \mathbb{X} \mid u = (h_1, h_2, h_3)^T \in \mathbb{R}^3\}$, $\text{Im} L = \{u \in \mathbb{Y} \mid \int_0^\omega u_i(t) dt = 0 \ (i \geq 1)\}$, and $\dim \text{Ker} L = 3 = \text{codim} \text{Im} L$. Since $\text{Im} L$ is closed in \mathbb{Y} , L is a Fredholm mapping of index zero. It is easy to show that P, Q are continuous projections such that $\text{Im} P = \text{Ker} L$, $\text{Im} L = \text{Ker} Q = \text{Im}(I - Q)$. Furthermore, the generalized inverse (to L) $K_P : \text{Im} L \rightarrow \text{Dom} L \cap \text{Ker} P$ exists and is given by

$$K_P \begin{bmatrix} u_1 \\ u_2 \\ u_3 \end{bmatrix} = \begin{bmatrix} \int_0^t u_1(s) ds - \frac{1}{T} \int_0^\omega \int_0^t u_1(s) ds dt \\ \int_0^t u_2(s) ds - \frac{1}{T} \int_0^\omega \int_0^t u_2(s) ds dt \\ \int_0^t u_3(s) ds - \frac{1}{T} \int_0^\omega \int_0^t u_3(s) ds dt \end{bmatrix}.$$

Obviously, QN and $K_P(I - Q)N$ are continuous. It is easy to see that N is L -compact on $\bar{\Omega}$ with any open bounded set $\Omega \subset \mathbb{X}$.

Now we will find an appropriate open, bounded subset Ω for application of the continuation theorem. Corresponding to the operator equation $Lu = \lambda Nu, \lambda \in (0, 1)$, we have

$$\begin{aligned} u'_1 &= \lambda \left[a_1 - b_1 \exp\{u_1\} - \frac{c_2 \exp\{u_2\}}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_2\}} - \frac{c_3 \exp\{u_3\}}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_3\}} \right], \\ u'_2 &= \lambda \left[-a_2 + \frac{d_2 \exp\{u_1\}}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_2\}} - b_2 \exp\{u_3\} \right], \\ u'_3 &= \lambda \left[-a_3 + \frac{d_3 \exp\{u_1\}}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_3\}} - b_3 \exp\{u_2\} \right]. \end{aligned} \tag{4.4.2}$$

Suppose that $(u_1, u_2, u_3) \in \mathbb{X}$ is an arbitrary solution of system (4.4.2) for a certain

$\lambda \in (0, 1)$. Integrating both sides of (4.4.2) over the interval $[0, \omega]$, we obtain

$$\begin{aligned} \hat{a}_1\omega &= \int_0^\omega \left[b_1 \exp\{u_1\} + \frac{c_2 \exp\{u_2\}}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_2\}} \right. \\ &\quad \left. + \frac{c_3 \exp\{u_3\}}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_3\}} \right] dt, \\ \hat{a}_i\omega + \int_0^\omega b_i \exp\{u_j\} dt &= \int_0^\omega \frac{d_i \exp\{u_1\} dt}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_i\}} \\ &\leq \int_0^\omega \frac{d_i}{\beta} dt = \widehat{\left(\frac{d_i}{\beta}\right)}\omega \quad (i, j \geq 2, i \neq j). \end{aligned} \quad (4.4.3)$$

It follows from (4.4.2) and (4.4.3) that for $i, j \geq 2$ ($i \neq j$),

$$\begin{aligned} \int_0^\omega |u_1(t)'| dt &\leq \lambda \left[\int_0^\omega a_1 dt + \int_0^\omega b_1 \exp\{u_1\} dt \right. \\ &\quad \left. + \int_0^\omega \frac{c_2 \exp\{u_2\}}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_2\}} dt \right. \\ &\quad \left. + \int_0^\omega \frac{c_3 \exp\{u_3\}}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_3\}} dt \right] \\ &< 2\hat{a}_1\omega, \\ \int_0^\omega |u_i(t)'| dt &< 2\widehat{\left(\frac{d_i}{\beta}\right)}\omega. \end{aligned}$$

Since $u \in \mathbb{X}$, there exist $\xi_i, \eta_i \in [0, \omega]$ such that

$$u_i(\xi_i) = \min_{t \in [0, \omega]} u_i(t), \quad u_i(\eta_i) = \max_{t \in [0, \omega]} u_i(t) \quad (i \geq 1). \quad (4.4.4)$$

From the first equation of (4.4.3) and (4.4.4), we obtain $\hat{a}_1\omega \geq \int_0^\omega b_1 \exp\{u_1(\xi_1)\} dt = \hat{b}_1\omega \exp\{u_1(\xi_1)\}$, from which follows $u_1(\xi_1) < L_{11}$. Hence

$$u_1(t) \leq u_1(\xi_1) + \int_0^\omega |u_1'(t)| dt < L_{11} + 2\hat{a}_1\omega = H_{11} \quad \text{for all } t \geq 0.$$

On the other hand, from the first equation of (4.4.3) and (4.4.4), we also have

$$\begin{aligned} \hat{a}_1\omega &\leq \int_0^\omega b_1 \exp\{u_1(\eta_1)\} dt + \int_0^\omega \frac{c_2(t) + c_3(t)}{\gamma(t)} dt \\ &= \left[\hat{b}_1 \exp\{u_1(\eta_1)\} + \widehat{\left(\frac{c_2 + c_3}{\gamma}\right)} \right] \omega. \end{aligned}$$

Then for any $t \geq 0$,

$$\begin{aligned} u_1(t) &\geq u_1(\eta_1) - \int_0^\omega |u_1'(t)| dt \\ &\geq \ln \left\{ \hat{a}_1 - \widehat{\left(\frac{c_2 + c_3}{\gamma}\right)} \right\} - 2\hat{a}_1\omega \\ &= H_{12}. \end{aligned}$$

From the arguments above, we have $H_{12} \leq u_1(t) \leq H_{11}$ for all $t \in [0, \omega]$. It then follows from the second equation of (4.4.3) and (4.4.4) that

$$\begin{aligned} \hat{a}_i \omega &\leq \int_0^\omega \frac{d_i \exp\{u_1\} dt}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_i\}} \\ &\leq \int_0^\omega \frac{d_i \exp\{H_{11}\} dt}{\alpha^l + \beta^l \exp\{H_{11}\} + \gamma^l \exp\{u_i(\xi_i)\}} \\ &= \frac{\omega \hat{d}_i \exp\{H_{11}\}}{\alpha^l + \beta^l \exp\{H_{11}\} + \gamma^l \exp\{u_i(\xi_i)\}}, \end{aligned}$$

from which implies

$$\begin{aligned} u_i(\xi_i) &\leq \ln \frac{(\hat{d}_i - \hat{a}_i \beta^l) \exp\{H_{11}\} - \hat{a}_i \alpha^l}{\hat{a}_i \gamma^l} \\ &= \ln \frac{\hat{a}_1 (\hat{d}_i - \hat{a}_i \beta^l) \exp\{2\hat{a}_1 \omega\} - \hat{a}_i \hat{b}_1 \alpha^l}{\hat{a}_i \hat{b}_1 \gamma^l}, \end{aligned}$$

and then

$$\begin{aligned} u_i(t) &\leq u_i(\xi_i) + \int_0^\omega |u'_i(t)| dt \\ &\leq \ln \frac{\hat{a}_1 (\hat{d}_i - \hat{a}_i \beta^l) \exp\{2\hat{a}_1 \omega\} - \hat{a}_i \hat{b}_1 \alpha^l}{\hat{a}_i \hat{b}_1 \gamma^l} + 2 \widehat{\left(\frac{\hat{d}_i}{\beta}\right)} \omega \\ &= H_{i1} \quad (i \geq 2). \end{aligned}$$

Similarly, for $i, j \geq 2$ ($i \neq j$) and $t \geq 0$, we have

$$\begin{aligned} \hat{a}_i \omega &= \int_0^\omega \left[\frac{d_i \exp\{u_1\}}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_i\}} - b_i \exp\{u_j\} \right] dt \\ &\geq \int_0^\omega \left[\frac{d_i \exp\{H_{12}\}}{\alpha^u + \beta^u \exp\{H_{12}\} + \gamma^u \exp\{u_i(\eta_i)\}} - b_i \exp\{H_{j1}\} \right] dt \\ &= \left[\frac{\hat{d}_i \exp\{H_{12}\}}{\alpha^u + \beta^u \exp\{H_{12}\} + \gamma^u \exp\{u_i(\eta_i)\}} - \hat{b}_i \exp\{H_{j1}\} \right] \omega, \end{aligned}$$

from which implies

$$u_i(\eta_i) \geq \ln \frac{d_i \exp\{H_{12}\} - (\alpha^u + \beta^u \exp\{H_{12}\})(\hat{a}_i + \hat{b}_i \exp\{H_{j1}\})}{\gamma^u (\hat{a}_i + \hat{b}_i \exp\{H_{j1}\})},$$

and

$$\begin{aligned} u_i(t) &\geq u_i(\eta_i) - \int_0^\omega |u'_i(t)| dt \\ &\geq \ln \frac{d_i \exp\{H_{12}\} - (\alpha^u + \beta^u \exp\{H_{12}\})(\hat{a}_i + \hat{b}_i \exp\{H_{j1}\})}{\gamma^u (\hat{a}_i + \hat{b}_i \exp\{H_{j1}\})} - 2 \widehat{\left(\frac{\hat{d}_i}{\beta}\right)} \omega \\ &= H_{i2}. \end{aligned}$$

Put $B_i = \max\{|H_{i1}|, |H_{i2}|\}$ ($i \geq 1$), then $\max_{t \in [0, \omega]} |u_i| \leq B_i$. Thus, for any solution $u \in \mathbb{X}$ of (4.4.2), we have $\|u\| \leq \sum_{i=1}^3 B_i$, and clearly, B_i ($i \geq 1$) are independent of λ . Taking $B = \sum_{i=1}^4 B_i$ where B_4 is taken sufficiently large such that $B_4 \geq \sum_{i=1}^3 \sum_{j=1}^2 |L_{ij}|$ and letting $\Omega = \{u \in \mathbb{X} \mid \|u\| < B\}$, then Ω satisfies the condition (a) of Lemma 4.12. To compute the Brouwer degree, let us consider the homotopy

$$H_\mu(u) = \mu QN(u) + (1 - \mu)G(u), \quad \mu \in [0, 1],$$

where $G : \mathbb{R}^3 \rightarrow \mathbb{R}^3$,

$$G(u) = \begin{bmatrix} \hat{a}_1 - \hat{b}_1 \exp\{u_1\} \\ -\hat{a}_2 - \hat{b}_2 \exp\{u_3\} + \frac{1}{\omega} \int_0^\omega \frac{d_2(t) \exp\{u_1\} dt}{\alpha + \beta \exp\{u_2\} + \gamma \exp\{u_2\}} \\ -\hat{a}_3 - \hat{b}_3 \exp\{u_2\} + \frac{1}{\omega} \int_0^\omega \frac{d_3(t) \exp\{u_1\} dt}{\alpha + \beta \exp\{u_3\} + \gamma \exp\{u_3\}} \end{bmatrix}.$$

We have

$$H_\mu(u) = \begin{bmatrix} \hat{a}_1 - \hat{b}_1 \exp\{u_1\} - \frac{1}{\omega} \int_0^\omega \left[\frac{\mu c_2 \exp\{u_2\}}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_2\}} + \frac{\mu c_3 \exp\{u_3\}}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_3\}} \right] dt \\ -\hat{a}_2 - \hat{b}_2 \exp\{u_3\} + \frac{1}{\omega} \int_0^\omega \frac{d_2 \exp\{u_1\} dt}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_2\}} \\ -\hat{a}_3 - \hat{b}_3 \exp\{u_2\} + \frac{1}{\omega} \int_0^\omega \frac{d_3 \exp\{u_1\} dt}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_3\}} \end{bmatrix}.$$

By carrying out similar arguments as above, one can easily show that any solution u^* of the equation $H_\mu(u) = \mathbf{0} \in \mathbb{R}^3$ with $\mu \in [0, 1]$ satisfies $L_{i1} \leq u_i^* \leq L_{i2}$ ($i \geq 1$). Thus, $\mathbf{0} \notin H_\mu(\partial\Omega \cap \text{Ker}L)$ for $\mu \in [0, 1]$, and then $QN(\partial\Omega \cap \text{Ker}L) \neq \mathbf{0}$. Note that the isomorphism J can be the identity mapping I , since $\text{Im}P = \text{Ker}L$, by the invariance property of homotopy, we have

$$\begin{aligned} & \deg(JQN, \Omega \cap \text{Ker}L, \mathbf{0}) \\ &= \deg(QN, \Omega \cap \text{Ker}L, \mathbf{0}) \\ &= \deg(QN, \Omega \cap \mathbb{R}^3, \mathbf{0}) \\ &= \deg(G, \Omega \cap \mathbb{R}^3, \mathbf{0}) \\ &= \text{sgn} \left\{ \det \begin{bmatrix} -\hat{b}_1 \exp\{u_1\} & 0 & 0 \\ \frac{\partial f_2(u_1, u_2)}{\partial u_1} & \frac{\partial f_2(u_1, u_2)}{\partial u_2} & -\hat{b}_2 \exp\{u_3\} \\ \frac{\partial f_3(u_1, u_3)}{\partial u_1} & -\hat{b}_3 \exp\{u_2\} & \frac{\partial f_3(u_1, u_3)}{\partial u_3} \end{bmatrix} \right\} \\ &= -\text{sgn} \left\{ \hat{b}_1 \exp\{u_1\} \left(\frac{\partial f_2(u_1, u_2)}{\partial u_2} \frac{\partial f_3(u_1, u_3)}{\partial u_3} + \hat{b}_2 \hat{b}_3 \exp\{u_2 + u_3\} \right) \right\}, \end{aligned} \tag{4.4.5}$$

where $\deg(\cdot, \cdot, \cdot)$ is the Brouwer degree [79] and

$$f_2(u_1, u_2) = \frac{1}{\omega} \int_0^\omega \frac{d_2 \exp\{u_1\} dt}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_2\}},$$

$$f_3(u_1, u_3) = \frac{1}{\omega} \int_0^\omega \frac{d_3 \exp\{u_1\} dt}{\alpha + \beta \exp\{u_1\} + \gamma \exp\{u_3\}}.$$

It is easy to see that functions $f_i(u_1, u_i)$ are decreasing in $u_i \in \mathbb{R}$ ($i \geq 2$). Then

$$\frac{\partial f_2(u_1, u_2)}{\partial u_2} \frac{\partial f_3(u_1, u_3)}{\partial u_3} > 0. \tag{4.4.6}$$

Combining (4.4.5) and (4.4.6) gives $\deg(JQN, \Omega \cap \text{Ker}L, \mathbf{0}) = -1 \neq 0$. By now we have proved that Ω verifies all requirements of Lemma 4.12, then $Lu = Nu$ has at least one solution in $\text{Dom}L \cap \bar{\Omega}$, i.e., (4.4.1) has at least one ω -periodic solution u^* in $\text{Dom}L \cap \bar{\Omega}$. Set $x_i^* = \exp\{u_i^*\}$ ($i \geq 1$), then x^* is an ω -periodic solution of system (4.1.1) with strictly positive components. We complete the proof. \square

Corollary 4.14. *If the ω -periodic solution x^* in Theorems 4.13 satisfies the assumptions in Theorems 4.11, then x^* is globally asymptotically stable.*

Proof. The proof of this corollary are derived directly from Theorems 4.11 and 4.13. \square

4.5 Numerical examples and conclusion

In this section, we present some numerical examples. At the first example, we consider the case $a_1 = 4.7 + \sin(\pi t)$, $b_1 = 2.4 - \cos(2.7t)$, $c_2 = 10.1 + 2.2 \sin(1.4t)$, $c_3 = 9.3 + \cos(2.8t)$, $a_2 = (1.1 - \cos(2\pi t))/2.5$, $b_2 = 1.4 + \sin(0.8t)$, $d_2 = 9.9 - 0.4 \sin(0.6t)$, $a_3 = (2.2 - \cos(1.7t))/6$, $b_3 = (2.3 + 1.3 \sin(3.2t))/2$, $d_3 = 8.5 + \sin(0.9\pi t)$, $\alpha = (1.2 - \cos(2t))/4$, $\beta = (2.3 + \cos(1.2t))/5$, $\gamma = 5.5 - 0.5 \sin(t)$. By (4.3.1), $M_i^0 > 0$, $m_i^0 > 0$ ($i \geq 1$) then Hypothesis 4.6 holds and system (4.1.1) has invariant set. Figure 4.1 is the orbit of solution with initial value $x^0 = (1.3, 1.4, 1.1)$, it seems to be very chaotic but it is permanent. According to theorem 4.11, it is not only permanent but also globally asymptotically stable. In spite of different initial value, $\tilde{x}^0 = (1.3, 1.4, 1.1)$ and $\bar{x}^0 = (0.6, 1, 1.5)$, solution \tilde{x}_i and \bar{x}_i ($i \geq 1$) still tend to one trajectory (see Figures 4.2-4.4).

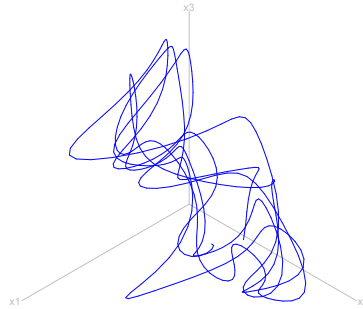
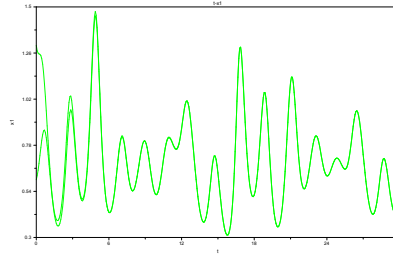
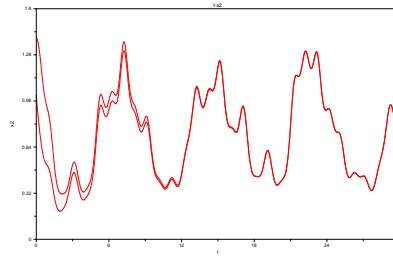
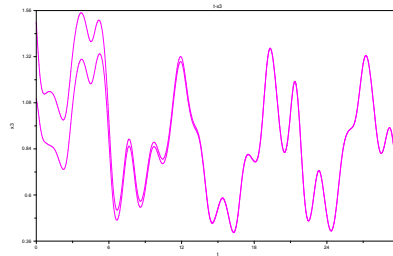


Figure 4.1: Orbit of globally asymptotically stable system

In next example, Theorem 4.9 will be illustrated by system (4.1.1) with coefficients $a_1 = 3 + 1.2 \sin(2.4t)$, $b_1 = 2.4 + 2 \cos(\pi t)$, $c_2 = 5.1 - 0.9 \sin(1.7\pi t)$, $c_3 = 4.4 - 1.2 \cos(\pi t)$, $a_2 = 1.1 - \cos(1.9t)$, $b_2 = (2.6 + \sin(3\pi t))/4$, $d_2 = 4.3 - 1.7 \sin(0.5\pi t)$, $a_3 = 2.1 - 2.5 \cos(1.4\pi t)$, $b_3 = 0.8 - 1.3 \sin(1.6t)$, $d_3 = 2.9 + 2.3 \sin(0.4t)$, $\alpha = (1.8 - \cos(5.7t))/3$, $\beta = 1 - 0.2 \cos(0.2\pi t)$, $\gamma = 3.4 - 1.6 \sin(1.8t)$ and initial condition $x^0 = (1.3, 2.1, 2.4)$. Since $M_3^0 < 0$ then the density of species X_3 goes extinct (see

Figure 4.2: Population sizes X_1 with respect to timeFigure 4.3: Population sizes X_2 with respect to timeFigure 4.4: Population sizes X_3 with respect to time

Figures 4.5-4.6). Therefore, the predator X_3 vanishes and system (4.1.1) is not permanent.

For the model with periodic coefficients, we consider the last example concerning the numerical solutions of system (4.1.1) where $a_1 = 3 + 1.3 \sin(2t)$, $b_1 = 2.2 + 1.9 \cos(2t)$, $c_2 = 2.8(2.2 - \sin(2t))$, $c_3 = (3.5 - 2 \cos(2t))/2$, $a_2 = 1 - 0.6 \cos(2t)$, $b_2 = 1.2 + 0.5 \sin(2t)$, $d_2 = 4 + 1.8 \sin(2t)$, $a_3 = (1.2 - \cos(2t))/3$, $b_3 = 1.4 + 1.1 \sin(2t)$, $d_3 = 3.1 - 2.3 \sin(2t)$, $\alpha = 0.1(3.2 - 2 \cos(2t))$, $\beta = (2.1 + 1.8 \cos(2t))/5$, $\gamma = 3.3 - \sin(2t)$ and initial value $x^0 = (1.1, 1.9, 1.4)$. Under π -periodic perturbation satisfying Theorem 4.13, system (4.1.1) has positive π -periodic solution (see Figures 4.7-4.8). Moreover, the hypothesis of Theorem 4.11 also holds then it is globally asymptotically stable.

In conclusion, this work provides some results about the asymptotic behavior

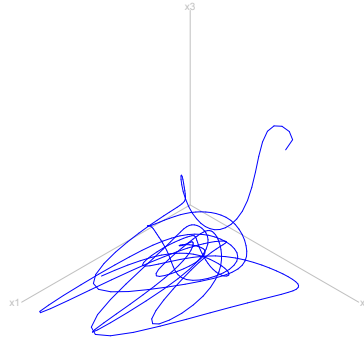


Figure 4.5: Orbit of non permanent system

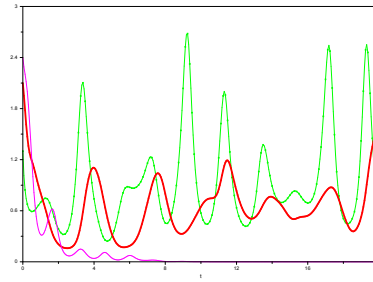


Figure 4.6: Orbit of non permanent system with respect to time

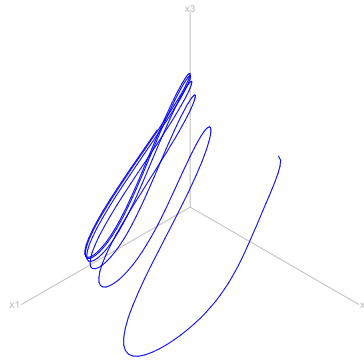


Figure 4.7: Orbit of periodic system

of a model of one prey and two predators with Beddington - DeAngelis functional responses. The mathematical analysis presented in this model shows that according to the value of the coefficients, one can make suitable predictions about the asymptotic behavior of the overall predator-prey system including the permanence, the periodicity, the global asymptotic stability and specially the extinction of species. Those conclusions warn us to have a timely decision to protect species in our ecolog-

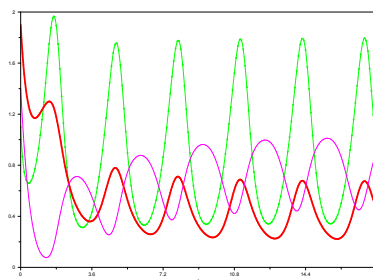


Figure 4.8: Orbit of periodic system with respect to time

ical system. Further, the given conditions on coefficients can be easily numerically computed.

Chapter 5

Population dynamics in random environments

5.1 Dynamical behavior of a stochastic SIRS epidemic model

5.1.1 Introduction

This section details paper [111]. The dynamics of disease spreading among a population have been investigated very widely in the frame of deterministic models e.g. [25], [39], [86], [105]. In such deterministic models, the environment is assumed to be constant. However, in most real situations, it is necessary to take into account random change of environmental conditions and their effects on the spread of the disease. For instance, the disease can be more likely to spread in wet (cold) condition rather than in dry (hot) condition or any other characteristics of the environment that may change randomly. Therefore, it is important to consider the disease dynamics under the impact of randomness of environmental conditions. There are many papers about this topic in recent years e.g. [9], [63], [76], [84].

The basic simplest epidemic model that we consider is the classical SIRS model introduced by Kermack-McKendrick of the form (see [86] for details)

$$\begin{cases} \dot{S} = -aSI + cR \\ \dot{I} = aSI - bI \\ \dot{R} = bI - cR, \end{cases} \quad (5.1.1)$$

where the susceptible (S), infective (I) and removed (R) classes are three compartments of the total population N . Transitions between these compartments are denoted respectively by a , b , and c . They describe the course of the transmission, recovery and loss of immunity.

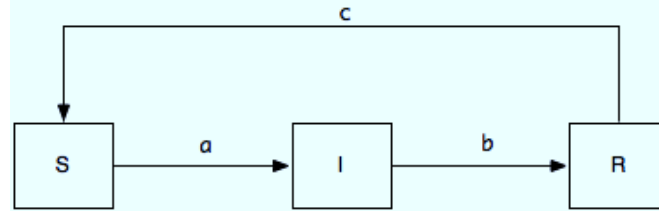


Figure 5.1: SIRS diagram.

In further studying the SIRS model, we note that the sum $S + I + R = N$ and it is a constant of population size. So that for convenience the removed class (R) can always be eliminated. The reduction of the equation (5.1.1) is then

$$\begin{cases} \dot{S} = -aSI + c(N - S - I) \\ \dot{I} = aSI - bI. \end{cases} \quad (5.1.2)$$

It is easy to analyze the previous simple system (5.1.2) and to show that two situations can occur (see [66], [86], [98]):

- If the basic reproduction number $\mathcal{R}_0 = \frac{Na}{b} > 1$ the disease spreads among the population and a positive equilibrium (s_*, i_*) is globally asymptotically stable. It is therefore an endemic situation.
- If $\mathcal{R}_0 = \frac{Na}{b} < 1$ the disease is eradicated as a disease free equilibrium $(N, 0)$, which is asymptotically stable. This situation is the eradication of the disease among the population.

In this work, we shall concentrate on the switching two classical Kernack and MacKendrick SIRS model, which will be chosen as the basic models for the epidemics. We shall assume that there are two environmental states in each of which the system evolves according to a deterministic differential equation and that the system switches randomly between these two states. Thus, we can suppose there is a telegraph noise affecting on the model in the form of switching between two-element set, $E = \{+, -\}$. With different states, the disease dynamics are different. The stochastic displacement of environmental conditions provokes model to change from the system in state $+$ to the system in state $-$ and vice versa.

Several questions naturally arise. For instance, in the case where the disease spreads in an environmental condition, while it is vanished in the other one, what will be the global and asymptotic behavior of the system? Using the basic reproduction number \mathcal{R}_0 of both models and the switching intensities, can we make predictions about the asymptotic behavior of the global system, i.e., the existence of a global endemic state or a disease free state?

This section has 5 subsections. Subsection 5.1.2 details the model and gives some properties of the boundary equations. In Subsection 5.1.3, dynamic behavior of the solutions is studied and the ω -limit sets are completely described for each case. It is shown that the threshold λ which will be given later plays an important role to determine whether the disease will vanish or be persistent. In Subsection

5.1.4, we study stability in distribution of the system. In the last subsection 5.1.5, some simulation results illustrate the behavior of the SIRS model under telegraph noise. The conclusion presents a summary of the results and some perspectives of the work.

5.1.2 Preliminary

Let us consider a continuous-time Markov process ξ_t , $t \in \mathbb{R}_+$, defined on the probability space $(\Omega, \mathcal{F}, \mathbb{P})$, with values in the set of two elements, say $E = \{+, -\}$. Suppose that (ξ_t) has the transition intensities $+\xrightarrow{\alpha}-$ and $-\xrightarrow{\beta}+$ with $\alpha > 0, \beta > 0$. The process (ξ_t) , say "telegraph noise", has a unique stationary distribution

$$p = \lim_{t \rightarrow \infty} \mathbb{P}\{\xi_t = +\} = \frac{\beta}{\alpha + \beta}; \quad q = \lim_{t \rightarrow \infty} \mathbb{P}\{\xi_t = -\} = \frac{\alpha}{\alpha + \beta}.$$

The trajectory of (ξ_t) is piecewise constant, cadlag functions. Suppose that

$$0 = \tau_0 < \tau_1 < \tau_2 < \dots < \tau_n < \dots$$

are its jump times. Put

$$\sigma_1 = \tau_1 - \tau_0, \sigma_2 = \tau_2 - \tau_1, \dots, \sigma_n = \tau_n - \tau_{n-1} \dots$$

It is known that, if ξ_0 is given, (σ_n) is a sequence of independent random variables. Moreover, if $\xi_0 = +$ then σ_{2n+1} has the exponential density $\alpha 1_{[0, \infty)} \exp(-\alpha t)$ and σ_{2n} has the density $\beta 1_{[0, \infty)} \exp(-\beta t)$. Conversely, if $\xi_0 = -$ then σ_{2n} has the exponential density $\alpha 1_{[0, \infty)} \exp(-\alpha t)$ and σ_{2n+1} has the density $\beta 1_{[0, \infty)} \exp(-\beta t)$ (see [60, vol. 2, pp. 217]). Here $1_{[0, \infty)} = 1$ for $t \geq 0$ ($= 0$ for $t < 0$).

In this section, we consider the Kernack-MacKendrick model under the telegraph noise ξ_t of the form:

$$\begin{cases} \dot{S} = -a(\xi_t)SI + c(\xi_t)(N - S - I) \\ \dot{I} = a(\xi_t)SI - b(\xi_t)I \end{cases}, \quad (5.1.3)$$

where $g : E = \{+, -\} \rightarrow \mathbb{R}_+$ for $g = a, b, c$. The noise (ξ_t) carries out a switching between two deterministic systems

$$\begin{cases} \dot{S} = -a(+)SI + c(+)(N - S - I) \\ \dot{I} = a(+)SI - b(+)I, \end{cases} \quad (5.1.4)$$

and

$$\begin{cases} \dot{S} = -a(-)SI + c(-)(N - S - I) \\ \dot{I} = a(-)SI - b(-)I. \end{cases} \quad (5.1.5)$$

Since (ξ_t) takes values in a two-element set E , if the solution of (5.1.3) satisfies equation (5.1.4) on the interval (τ_{n-1}, τ_n) , then it must satisfy equation (5.1.5) on

the interval (τ_n, τ_{n+1}) and vice versa. Therefore, $(S(\tau_n), I(\tau_n))$ is the switching point, that is the terminal point of one state and simultaneously the initial condition of the other. It is known that with positive initial values, solutions to both (5.1.4) and (5.1.5) remain nonnegative for all $t \geq 0$. Thus, any solution to (5.1.3) starting in $\text{int}\mathbb{R}_+^2$ exists for all $t \geq 0$ and remain nonnegative.

It is easily verified that the systems (5.1.4) and (5.1.5) respectively have the equilibrium points

$$(s_*^\pm, i_*^\pm) = \left(\frac{b(\pm)}{a(\pm)}, \frac{c(\pm)(N - \frac{b(\pm)}{a(\pm)})}{b(\pm) + c(\pm)} \right), \quad (5.1.6)$$

and their global dynamics depend on these equilibriums. Concretely, if $i_*^\pm > 0$ then these positive equilibriums are asymptotically stable, i.e., when $N > \frac{b(\pm)}{a(\pm)}$, $\lim_{t \rightarrow \infty} (S^\pm(t), I^\pm(t)) = (s_*^\pm, i_*^\pm)$. This is the endemic case, both susceptible and infective classes are together present. On the contrary, if $N \leq \frac{b(\pm)}{a(\pm)}$ then $\lim_{t \rightarrow \infty} (S^\pm(t), I^\pm(t)) = (N, 0)$ and the infective class will disappear. It is called the free case

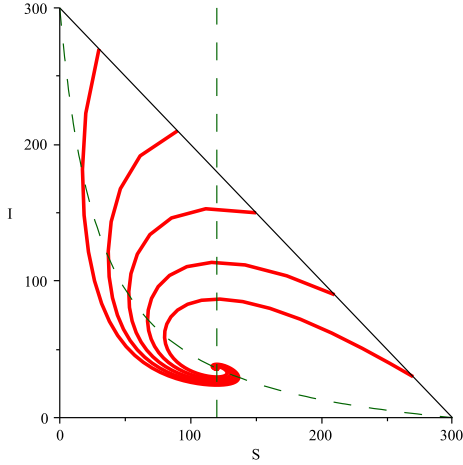


Figure 5.2: An example of endemic case

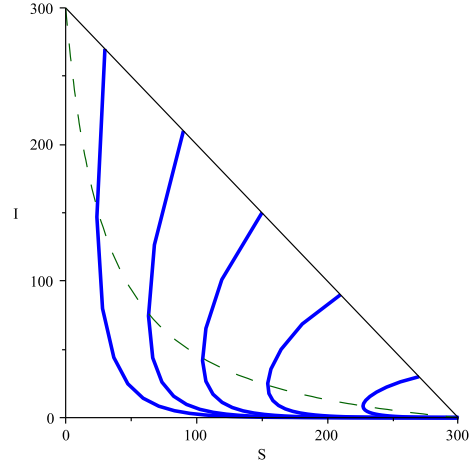


Figure 5.3: An example of disease free case.

5.1.3 Dynamical behavior of solutions

For any $(s_0, i_0) \in \text{int}\mathbb{R}_+^2$ with $s_0 + i_0 \leq N$, we denote by $(S(t, s_0, i_0), I(t, s_0, i_0))$ the solution of (5.1.3) satisfying the initial condition $(S(0, s_0, i_0), I(0, s_0, i_0)) = (s_0, i_0)$. For the sake of simplicity, we write $(S(t), I(t))$ for $(S(t, s_0, i_0), I(t, s_0, i_0))$ if there is no confusion. A function f defined on $[0, \infty)$ is said to be ultimately bounded above (respectively, ultimately bounded below) by m if $\limsup_{t \rightarrow \infty} f(t) < m$ (respectively, $\liminf_{t \rightarrow \infty} f(t) > m$).

It is easy to see that the triangle $\nabla := \{(s, i) : s \geq 0, i \geq 0; s + i \leq N\}$ is invariant for the system (5.1.3). In the future, without loss of generality, suppose that $\frac{b(+)}{a(+)} \leq \frac{b(-)}{a(-)}$.

Define

$$\lambda = p(a(+)N - b(+)) + q(a(-)N - b(-)). \quad (5.1.7)$$

Proposition 5.1.1.

a) If $\lambda > 0$ then there is a $\delta_1 > 0$ such that $\limsup_{t \rightarrow \infty} I(t) > \delta_1$.

b) If $\lambda < 0$ then $\lim_{t \rightarrow \infty} I(t) = 0$ and $\lim_{t \rightarrow \infty} S(t) = N$.

Proof. a) The second equation of the system (5.1.3) follows

$$\frac{\ln I(t) - \ln I(0)}{t} = \frac{1}{t} \int_0^t (a(\xi_{\bar{t}})S(\bar{t}) - b(\xi_{\bar{t}}))d\bar{t}.$$

Since $I(t) \leq N$, $\limsup_{t \rightarrow \infty} \frac{\ln I(t) - \ln I(0)}{t} \leq 0$. Therefore,

$$\begin{aligned} \limsup_{t \rightarrow \infty} \left(\frac{1}{t} \int_0^t (a(\xi_{\bar{t}})N - b(\xi_{\bar{t}}))d\bar{t} - \frac{1}{t} \int_0^t a(\xi_{\bar{t}})(N - S(\bar{t}))d\bar{t} \right) = \\ \limsup_{t \rightarrow \infty} \frac{1}{t} \int_0^t (a(\xi_{\bar{t}})S(\bar{t}) - b(\xi_{\bar{t}}))d\bar{t} \leq 0. \end{aligned}$$

Thus,

$$\liminf_{t \rightarrow \infty} \frac{1}{t} \int_0^t (a(\xi_{\bar{t}})N - b(\xi_{\bar{t}}))d\bar{t} \leq \liminf_{t \rightarrow \infty} \frac{1}{t} \int_0^t a(\xi_{\bar{t}})(N - S(\bar{t}))d\bar{t}.$$

Because the process (ξ_t) has a unique stationary distribution $\lim_{t \rightarrow \infty} \mathbb{P}\{\xi_t = +\} = p$ and $\lim_{t \rightarrow \infty} \mathbb{P}\{\xi_t = -\} = q$, then by the law of large numbers

$$\lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t (a(\xi_{\bar{t}})N - b(\xi_{\bar{t}}))d\bar{t} = p(a(+)N - b(+)) + q(a(-)N - b(-)) = \lambda.$$

Denote $g_{\min} = \min(g(+), g(-))$, $g_{\max} = \max(g(+), g(-))$ for $g = a, b, c$. We have

$$\begin{aligned} \liminf_{t \rightarrow \infty} \frac{1}{t} \int_0^t a_{\max}(N - S(\bar{t}))d\bar{t} &\geq \liminf_{t \rightarrow \infty} \frac{1}{t} \int_0^t a(\xi_{\bar{t}})(N - S(\bar{t}))d\bar{t} \\ &\geq \liminf_{t \rightarrow \infty} \frac{1}{t} \int_0^t a(\xi_{\bar{t}})(N - b(\xi_{\bar{t}}))d\bar{t} = \lambda. \end{aligned} \quad (5.1.8)$$

On the other hand, from

$$\dot{S}(t) = -(a(\xi_t)S(t) + c(\xi_t))I(t) + c(\xi_t)(N - S(t)) \geq -(a(\xi_t)N + c(\xi_t))I(t) + c(\xi_t)(N - S(t)),$$

it follows

$$\frac{S(t) - S(0)}{t} \geq \frac{1}{t} \int_0^t -(a(\xi_{\bar{t}})N + c(\xi_{\bar{t}}))I(\bar{t})d\bar{t} + \frac{1}{t} \int_0^t c(\xi_{\bar{t}})(N - S(\bar{t}))d\bar{t}.$$

Since $\lim_{t \rightarrow \infty} \frac{S(t) - S(0)}{t} = 0$,

$$\limsup_{t \rightarrow \infty} \left(\frac{1}{t} \int_0^t -(a(\xi_{\bar{t}})N + c(\xi_{\bar{t}}))I(\bar{t})d\bar{t} + \frac{1}{t} \int_0^t c(\xi_{\bar{t}})(N - S(\bar{t}))d\bar{t} \right) \leq 0.$$

Hence,

$$\begin{aligned} \liminf_{t \rightarrow \infty} \frac{1}{t} \int_0^t (a_{\max}N + c_{\max})I(\bar{t})d\bar{t} &\geq \liminf_{t \rightarrow \infty} \frac{1}{t} \int_0^t (a(\xi_{\bar{t}})N + c(\xi_{\bar{t}}))I(\bar{t})d\bar{t} \\ &\geq \liminf_{t \rightarrow \infty} \frac{1}{t} \int_0^t c(\xi_{\bar{t}})(N - S(\bar{t}))d\bar{t} \geq \liminf_{t \rightarrow \infty} \frac{1}{t} \int_0^t c_{\min}(N - S(\bar{t}))d\bar{t}. \end{aligned} \quad (5.1.9)$$

Combining (5.1.8) and (5.1.9), we obtain

$$\begin{aligned} \liminf_{t \rightarrow \infty} \frac{1}{t} \int_0^t I(\bar{t})d\bar{t} &\geq \liminf_{t \rightarrow \infty} \frac{1}{t} \int_0^t \frac{c_{\min}}{a_{\max}N + c_{\max}}(N - S(\bar{t}))d\bar{t} \\ &\geq \frac{c_{\min}}{(a_{\max}N + c_{\max})a_{\max}} \lambda > 0. \end{aligned}$$

This inequality implies that there exists $\delta_1 > 0$ such that $\limsup_{t \rightarrow \infty} I(t) > \delta_1$.

b) From the inequality

$$\frac{\dot{I}(t)}{I(t)} = a(\xi_t)S(t) - b(\xi_t) \leq a(\xi_t)N - b(\xi_t),$$

we have

$$\limsup_{t \rightarrow \infty} \frac{\ln I(t) - \ln I(0)}{t} \leq \limsup_{t \rightarrow \infty} \frac{1}{t} \int_0^t (a(\xi_{\bar{t}})S(\bar{t}) - b(\xi_{\bar{t}}))d\bar{t} \leq \lambda < 0,$$

which implies that $\lim_{t \rightarrow \infty} I(t) = 0$. On the other hand,

$$\dot{S}(t) = -a(\xi_t)S(t)I(t) + c(\xi_t)(N - S(t) - I(t)) \geq -a_{\max}NI(t) + c_{\min}(N - S(t) - I(t)).$$

Thus,

$$S(t) \geq \int_0^t e^{-c_{\min}(t-\bar{t})}(-a_{\max}N + c_{\min})I(\bar{t})d\bar{t} + S(0)e^{-c_{\min}t} + c_{\min}N \int_0^t e^{-c_{\min}(t-\bar{t})}d\bar{t}.$$

We see that $\lim_{t \rightarrow \infty} \int_0^t e^{-c_{\min}(t-\bar{t})}d\bar{t} = \frac{1}{c_{\min}}$. Further, by paying attention that $\lim_{t \rightarrow \infty} I(t) = 0$ we also obtain

$$\lim_{t \rightarrow \infty} \int_0^t e^{-c_{\min}(t-\bar{t})}(-a_{\max}N + c_{\min})I(\bar{t})d\bar{t} = 0.$$

Hence, $\liminf_{t \rightarrow \infty} S(t) \geq N$. Combining $S(t) \leq N$ for all $t > 0$ gets $\lim_{t \rightarrow \infty} S(t) = N$. The proof is complete. \square

By definition of λ in (5.1.7) we have the following corollary.

Corollary 5.1.2. *If $\frac{b(+)}{a(+)} \geq N$ then $\lim_{t \rightarrow \infty} I(t) = 0$ and $\lim_{t \rightarrow \infty} S(t) = N$.*

In view of this corollary, in the following we suppose that $\frac{b(+)}{a(+)} < N$.

Proposition 5.1.3. *$S(t)$ is ultimately bounded below by $S_{\min} > 0$ and there is an invariant set for the system (5.1.3), which absorbs all positive solutions.*

Proof. Let S_{\min} be chosen such that

$$-Na(\pm)S_{\min} + c(\pm)\left(\frac{b(+)}{2a(+)} - S_{\min}\right) > m > 0, \quad (5.1.10)$$

and let $A = (S_{\min}, 0)$, $B = (S_{\min}, N - \frac{b(+)}{2a(+)}), C = (\frac{b(+)}{2a(+)}, N - \frac{b(+)}{2a(+)}), D = (N, 0)$. In the interior of the triangle ∇ we have $\dot{I}(t) = a(\xi_t)(S(t) - \frac{b(\xi_t)}{a(\xi_t)})I(t) \leq a(\xi_t)(S(t) - \frac{b(+)}{a(+)})I(t) \leq a(\xi_t)(\frac{b(+)}{2a(+)} - \frac{b(+)}{a(+)})I(t) = -a(\xi_t)\frac{b(+)}{2a(+)}I(t) < 0$ for all points lying above the line BC , whereas $\dot{S} > m$ for all points that are below the line BC and on the left of AB by (5.1.10) (see the figure 5.4). Therefore, it is easy to see that the quadrangle $ABCD$ is invariant under system (5.1.3) and all positive solutions ultimately go there. \square

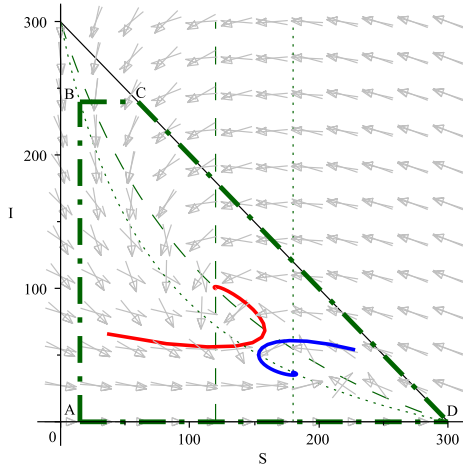


Figure 5.4: An example of invariant set. The invariant set is defined by 4 dash dot lines.

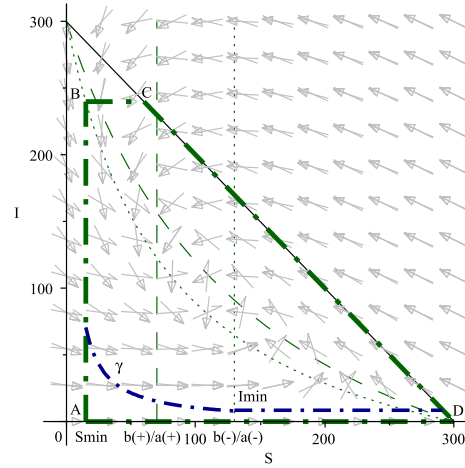


Figure 5.5: An example of existence of I_{\min} when $\frac{b(+)}{a(+)} < \frac{b(-)}{a(-)} < N$.

Definition 5.1.4.

1) System (5.1.3) is said to be *persistent* if $\limsup_{t \rightarrow \infty} S(t) > 0$, $\limsup_{t \rightarrow \infty} I(t) > 0$ for all solutions of (5.1.3).

2) In case there exists a positive ϵ such that

$$\begin{aligned}\epsilon &\leq \liminf_{t \rightarrow \infty} S(t) \leq \limsup_{t \rightarrow \infty} S(t) \leq 1/\epsilon, \\ \epsilon &\leq \liminf_{t \rightarrow \infty} I(t) \leq \limsup_{t \rightarrow \infty} I(t) \leq 1/\epsilon,\end{aligned}$$

we call the system (5.1.3) is *permanent*.

Corollary 5.1.5. *If $\lambda > 0$ then the system (5.1.3) is persistent.*

Proof. This result follows immediately from Propositions 5.1.1 and 5.1.3. \square

Proposition 5.1.6. *$I(t)$ is ultimately bounded below by $I_{\min} > 0$ if $\frac{b(-)}{a(-)} < N$.*

Proof. Since $\frac{b(-)}{a(-)} < N$, we can find an $0 < \varepsilon_0 < \delta_1$ such that $\min \{ -a(\pm)si + c(\pm)(N - s - i) > 0 : 0 < s \leq \frac{b(-)}{a(-)}, 0 < i \leq \varepsilon_0 \} > 0$. Then, while $I(t) \leq \varepsilon_0$ and $S(t) \leq \frac{b(-)}{a(-)}$ we have $\dot{S} > 0$ and $\frac{\dot{I}}{\dot{S}} = \frac{(a(\xi_t)S - b(\xi_t))I}{-a(\xi_t)SI + c(\xi_t)(N - S - I)} > -kI$ where k is some positive number. Denote by γ the piece of the solution curve to the equation $\frac{dI}{dS} = -kI$ starting at $(S_{\min}, \varepsilon_0)$ and ending at the intersection point $(\frac{b(-)}{a(-)}, \varepsilon_1)$ of this solution curve with the line $s = \frac{b(-)}{a(-)}$ (see the figure 5.5). Let G be the subdomain of quadrangle ABCD consisting of all $(s, i) \in ABCD$ lying above the curve γ if $s \leq \frac{b(-)}{a(-)}$ and lying above the line $i = \varepsilon_1$ if $\frac{b(-)}{a(-)} \leq s \leq N$. Obviously, G is invariant domain because $\frac{\dot{I}}{\dot{S}} > -kI, \dot{S} > 0$ on γ and $\dot{I} > 0$ on the segment $I = \varepsilon_1, \frac{b(-)}{a(-)} \leq S \leq N$. Since $\limsup_{t \rightarrow \infty} I(t) > \delta_1 > \varepsilon_0$ and $(S(t), I(t))$ must eventually enter the quadrangle ABCD, $(S(t), I(t))$ also eventually enters G which implies that $I(t)$ ultimately bounded below by $I_{\min} = \varepsilon_1$. \square

Corollary 5.1.7. *If $\frac{b(-)}{a(-)} < N$ then the system (5.1.3) is permanent.*

Adapted from the concept in [33], we define the (random) ω -limit set of the trajectory starting from an initial value (s_0, i_0) by

$$\Omega(s_0, i_0, \omega) = \bigcap_{T>0} \bigcup_{t>T} \overline{(S(t, s_0, i_0, \omega), I(t, s_0, i_0, \omega))}.$$

This concept is different from the one in [44] but it is closest to that of an ω -limit set for a deterministic dynamical system. In the case where $\Omega(s_0, i_0, \omega)$ is a.s constant, it is similar to the concept of weak attractor and attractor given in [95, 148]. Although, in general, the ω -limit set in this sense does not have the invariant property, this concept is appropriate for our purpose of describing the pathwise asymptotic behavior of the solution with a given initial value.

Our task in the next part is to describe the ω -limit sets of the system (5.1.3). Let $\pi_t^+(s, i) = (S^+(t, s, i), I^+(t, s, i))$, (resp. $\pi_t^-(s, i) = (S^-(t, s, i), I^-(t, s, i))$) be the solution of (5.1.4) (resp. (5.1.5)) starting in the point $(s, i) \in \mathbb{R}_+^2$.

From now on, let us fix an $(s_0, i_0) \in \mathbb{R}_+^2$ and suppose $\lambda > 0$. This implies that at least one of the systems (5.1.4), (5.1.5) has a globally asymptotically stable positive equilibrium. Without loss of generality, we assume the equilibrium point of the system (5.1.4) has this property, i.e., $\lim_{t \rightarrow \infty} \pi_t^+(s, i) = (s_*^+, i_*^+) \in \text{int } \mathbb{R}_+^2$ for any $(s, i) \in \text{int } \mathbb{R}_+^2$. Also, suppose that $\xi_0 = +$ with probability 1.

For $\varepsilon > 0$ small enough, denote by $\mathcal{U}_\varepsilon(s, i)$ the ε -neighborhood of (s, i) and by $H_\varepsilon \subset \mathbb{R}_+^2$ the compact set surrounded by AB, BC, CD and the line $i = \varepsilon$. Set

$$S_n = S(\tau_n, s_0, i_0); I_n = I(\tau_n, s_0, i_0), \mathcal{F}_0^n = \sigma(\tau_k : k \leq n); \mathcal{F}_n^\infty = \sigma(\tau_k - \tau_n : k > n).$$

We see that (S_n, I_n) is \mathcal{F}_0^n -adapted. Moreover, given ξ_0 , then \mathcal{F}_0^n is independent of \mathcal{F}_n^∞ .

Lemma 5.1.8. *Let $J \subsetneq \nabla$ be a compact set and $(s_*^+, i_*^+) \in J$. Then, for any $\delta_2 > 0$, there is a $T_1 = T_1(\delta_2) > 0$ such that $\pi_t^+(s, i) \in \mathcal{U}_{\delta_2}(s_*^+, i_*^+)$ for any $t \geq T_1$ and $(s, i) \in J$.*

Proof. Consider the system (5.1.4). Since (s_*^+, i_*^+) is asymptotically stable, we can find a $\bar{\delta}_2 = \bar{\delta}_2(\delta_2) > 0$ such that

$$\pi_t^+(\mathcal{U}_{\bar{\delta}_2}(s_*^+, i_*^+)) \subset \mathcal{U}_{\delta_2}(s_*^+, i_*^+) \quad \forall t \geq 0.$$

On the one hand, for $(s, i) \in J$, $\lim_{t \rightarrow \infty} \pi_t^+(s, i) = (s_*^+, i_*^+)$ which implies that there exists a T_{si} satisfying

$$\pi_t^+(s, i) \in \mathcal{U}_{\bar{\delta}_2/2}(s_*^+, i_*^+) \quad \text{for all } t \geq T_{si}.$$

By the continuous dependence of the solutions on the initial conditions, there is a neighborhood \mathcal{U}_{si} of (s, i) such that for any $(u, v) \in \mathcal{U}_{si}$ we have

$$\pi_{T_{si}}^+(u, v) \in \mathcal{U}_{\bar{\delta}_2}(s_*^+, i_*^+).$$

As a result,

$$\pi_t^+(u, v) \in \pi_{t-T_{si}}^+(\mathcal{U}_{\bar{\delta}_2}(s_*^+, i_*^+)) \subset \mathcal{U}_{\delta_2}(s_*^+, i_*^+) \quad \forall t \geq T_{si}.$$

Since J is compact and the family $\{\mathcal{U}_{si} : (s, i) \in J\}$ is an open covering of J , by Heine-Borel lemma, there is a finite subfamily, namely $\{\mathcal{U}_{s_i i_i}, i = 1, 2, \dots, n\}$, which covers J . Let $T_1 = \max_{1 \leq i \leq n} \{T_{s_i i_i}\}$. We see that if $(s, i) \in J$ then $\pi_t^+(s, i) \in \mathcal{U}_{\delta_2}(s_*^+, i_*^+)$ for any $t \geq T_1$. \square

Lemma 5.1.9. *There is a compact set $K \in \text{int } \mathbb{R}_+^2$ such that, with probability 1, there are infinitely many $k = k(\omega) \in \mathbb{N}$ satisfying $(S_{2k+1}, I_{2k+1}) \in K$.*

Proof. In the case $\frac{b(-)}{a(-)} < N$, we can choose $K \equiv G$, that was established in Proposition 5.1.6 and see that $(S_{2k+1}, I_{2k+1}) \in K$ for every $k > k_0$.

Suppose that $\frac{b(+)}{a(+)} < N < \frac{b(-)}{a(-)}$. With δ_1 is shown in Proposition 5.1.1, by a similar way to the construction of the set G in the proof of Proposition 5.1.6, we construct a curve γ^+ for the system (5.1.4), with the initial point (S_{\min}, δ_1) and the end point $(\frac{b(+)}{a(+)}, I_{\min}^+)$; then define the subdomain K of quadrangle $ABCD$ consisting of every $(s, i) \in ABCD$ lying above the curve γ^+ if $s \leq \frac{b(+)}{a(+)}$ and lying above the line $i = I_{\min}^+$ if $\frac{b(+)}{a(+)} \leq s \leq N$. It is seen that K is an invariant set for the system (5.1.4). By Proposition 5.1.1, there is a sequence $(\mu_n) \uparrow \infty$ such that $I(\mu_n) \geq \delta_1$ for all $n \in \mathbb{N}$. Further, since $I(t)$ is decreasing whenever $S(t) \leq \frac{b(+)}{a(+)}$, we can chose (μ_n) such that $S(\mu_n) > \frac{b(+)}{a(+)}$. If $\tau_{2k} \leq \mu_n < \tau_{2k+1}$, i.e. $\xi_{\mu_n} = +$, we have $(S_{2k+1}, I_{2k+1}) \in K$ because $(S(\mu_n), T(\mu_n)) \in K$ and K is invariant set for the system (5.1.4). For $\tau_{2k-1} \leq \mu_n < \tau_{2k}$, if $\sup_{\tau_{2k} \leq t < \tau_{2k+1}} I(t) \geq \delta_1$ we return to the above case. Otherwise, $I(t) < \delta_1$ for any $\tau_{2k} \leq t < \tau_{2k+2}$ since $I(t)$ is decreasing on $[\tau_{2k+1}, \tau_{2k+2})$... Continuing this process, we can either find an odd number $2m+1 > k$ such that $(S_{2m+1}, I_{2m+1}) \in K$ or see that $I(t) < \delta_1 \forall t > \tau_{2k}$. The latter contradicts to Proposition 5.1.1. The proof is complete. \square

Lemma 5.1.10. *Let $T_2 > 0$ and $(\bar{s}, \bar{i}) = \pi_{T_2}^-(s_*^+, i_*^+)$. For any $\delta_4 > 0$, there exist $\delta_3 > 0$ and $\bar{T}_2 > 0$ such that $\pi_t^-(u, v) \in \mathcal{U}_{\delta_4}(\bar{s}, \bar{i})$ for all $T_2 - \bar{T}_2 \leq t \leq T_2 + \bar{T}_2$ provided $(u, v) \in \mathcal{U}_{\delta_3}(s_*^+, i_*^+)$.*

Proof. This result is a consequence of Lemma 5.1.8 and the continuous dependence of the solutions on the initial values. \square

Lemma 5.1.11. *For any $\delta_6 > 0$ and $(s, i) \in H_\varepsilon$, there exists a $\delta_5 > 0$ such that $\pi_t^+(u, v) \in \mathcal{U}_{\delta_6}(\pi_t^+(s, i)) \forall t > 0$ (resp. $\pi_t^-(u, v) \in \mathcal{U}_{\delta_6}(\pi_t^-(s, i)) \forall t > 0$), where $(u, v) \in \mathcal{U}_{\delta_5}(s, i) \cap H_\varepsilon$.*

Proof. The conclusion follows straightforward from the continuous dependence of the solutions on the initial values. \square

To describe the pathwise dynamic behavior of the solutions of the system (5.1.3). Put

$$\Gamma = \left\{ (s, i) = \pi_{t_n}^{\varrho(n)} \cdots \pi_{t_2}^+ \pi_{t_1}^-(s_*^+, i_*^+) : 0 \leq t_1, t_2, \dots, t_n; n \in \mathbb{N} \right\}. \quad (5.1.11)$$

where $\varrho(k) = (-1)^k$.

Theorem 5.1.12. *If $\lambda > 0$ then for almost all ω , the closure $\bar{\Gamma}$ of Γ is a subset of $\Omega(s_0, i_0, \omega)$.*

Proof. With K is mentioned in Lemma 5.1.9, we construct a sequence

$$\begin{aligned}\eta_1 &= \inf\{2k+1 : (S_{2k+1}, I_{2k+1}) \in K\} \\ \eta_2 &= \inf\{2k+1 > \eta_1 : (S_{2k+1}, I_{2k+1}) \in K\} \\ &\dots \\ \eta_n &= \inf\{2k+1 > \eta_{n-1} : (S_{2k+1}, I_{2k+1}) \in K\} \dots\end{aligned}$$

It is easy to see that $\{\eta_k = n\} \in \mathcal{F}_0^n$ for any k, n . Thus the event $\{\eta_k = n\}$ is independent of \mathcal{F}_n^∞ if ξ_0 is given. By Lemma 5.1.9, $\eta_n < \infty$ a.s for all n .

Let $T_3 > 0, \bar{T}_3 > 0$. For any $k \in \mathbb{N}$, put $A_k = \{\sigma_{\eta_k+1} < T_3, \sigma_{\eta_k+2} > \bar{T}_3\}$. We have

$$\begin{aligned}\mathbb{P}(A_k) &= \mathbb{P}\{\sigma_{\eta_k+1} < T_3, \sigma_{\eta_k+2} > \bar{T}_3\} \\ &= \sum_{n=0}^{\infty} \mathbb{P}\{\sigma_{\eta_k+1} < T_3, \sigma_{\eta_k+2} > \bar{T}_3 \mid \eta_k = 2n+1\} \mathbb{P}\{\eta_k = 2n+1\} \\ &= \sum_{n=0}^{\infty} \mathbb{P}\{\sigma_{2n+2} < T_3, \sigma_{2n+3} > \bar{T}_3 \mid \eta_k = 2n+1\} \mathbb{P}\{\eta_k = 2n+1\} \\ &= \sum_{n=0}^{\infty} \mathbb{P}\{\sigma_{2n+2} < T_3, \sigma_{2n+3} > \bar{T}_3\} \mathbb{P}\{\eta_k = 2n+1\} \\ &= \sum_{n=0}^{\infty} \mathbb{P}\{\sigma_2 < T_3, \sigma_3 > \bar{T}_3\} \mathbb{P}\{\eta_k = 2n+1\} = \mathbb{P}\{\sigma_2 < T_3, \sigma_3 > \bar{T}_3\} > 0.\end{aligned}$$

Similarly,

$$\begin{aligned}\mathbb{P}(A_k \cap A_{k+1}) &= \mathbb{P}\{\sigma_{\eta_k+1} < T_3, \sigma_{\eta_k+2} > \bar{T}_3, \sigma_{\eta_{k+1}+1} < T_3, \sigma_{\eta_{k+1}+2} > \bar{T}_3\} \\ &= \sum_{0 \leq l < n < \infty} \mathbb{P}\{\sigma_{\eta_k+1} < T_3, \sigma_{\eta_k+2} > \bar{T}_3, \sigma_{\eta_{k+1}+1} < T_3, \sigma_{\eta_{k+1}+2} > \bar{T}_3 \mid \\ &\quad \eta_k = 2l+1, \eta_{k+1} = 2n+1\} \mathbb{P}\{\eta_k = 2l+1, \eta_{k+1} = 2n+1\} \\ &= \sum_{0 \leq l < n < \infty} \mathbb{P}\{\sigma_{2l+2} < T_3, \sigma_{2l+3} > \bar{T}_3, \sigma_{2n+2} < T_3, \sigma_{2n+3} > \bar{T}_3 \mid \eta_k = 2l+1, \\ &\quad \eta_{k+1} = 2n+1\} \times \mathbb{P}\{\eta_k = 2l+1, \eta_{k+1} = 2n+1\} \\ &= \sum_{0 \leq l < n < \infty} \mathbb{P}\{\sigma_{2n+2} < T_3, \sigma_{2n+3} > \bar{T}_3\} \mathbb{P}\{\sigma_{2l+2} < T_3, \sigma_{2l+3} > \bar{T}_3 \mid \\ &\quad \eta_k = 2l+1, \eta_{k+1} = 2n+1\} \times \mathbb{P}\{\eta_k = 2l+1, \eta_{k+1} = 2n+1\} \\ &= \sum_{0 \leq l < n < \infty} \mathbb{P}\{\sigma_2 < T_3, \sigma_3 > \bar{T}_3\} \mathbb{P}\{\sigma_{2l+2} < T_3, \sigma_{2l+3} > \bar{T}_3 \mid \\ &\quad \eta_k = 2l+1, \eta_{k+1} = 2n+1\} \times \mathbb{P}\{\eta_k = 2l+1, \eta_{k+1} = 2n+1\} \\ &= \mathbb{P}\{\sigma_2 < T_3, \sigma_3 > \bar{T}_3\} \sum_{0 \leq l < n < \infty} \mathbb{P}\{\sigma_{2l+2} < T_3, \sigma_{2l+3} > \bar{T}_3 \mid \\ &\quad \eta_k = 2l+1, \eta_{k+1} = 2n+1\} \times \mathbb{P}\{\eta_k = 2l+1, \eta_{k+1} = 2n+1\}\end{aligned}$$

$$\begin{aligned}
&= \mathbb{P}\{\sigma_2 < T_3, \sigma_3 > \bar{T}_3\} \sum_{l=0}^{\infty} \mathbb{P}\{\sigma_{2l+2} < T_3, \sigma_{2l+3} > \bar{T}_3 \mid \eta_k = 2l+1\} \mathbb{P}\{\eta_k = 2l+1\} \\
&= \mathbb{P}\{\sigma_2 < T_3, \sigma_3 > \bar{T}_3\}^2.
\end{aligned}$$

Therefore,

$$\mathbb{P}(A_k \cup A_{k+1}) = 1 - (1 - \mathbb{P}\{\sigma_2 < T_3, \sigma_3 > \bar{T}_3\})^2.$$

Continuing this way we obtain

$$\mathbb{P}\left(\bigcup_{i=k}^n A_i\right) = 1 - (1 - \mathbb{P}\{\sigma_2 < T_3, \sigma_3 > \bar{T}_3\})^{n-k+1}.$$

Hence,

$$\mathbb{P}\left(\bigcap_{k=1}^{\infty} \bigcup_{i=k}^{\infty} A_i\right) = \mathbb{P}\{\omega : \sigma_{\eta_n+1} < T_3, \sigma_{\eta_n+2} > \bar{T}_3 \text{ i.o. of } n\} = 1. \quad (5.1.12)$$

Fix $T_3 > 0$. From $\dot{I}(t) = a(\xi_t)S(t)I(t) - b(\xi_t)I(t) \geq -b_{\max}I(t)$ and $I(\tau_{\eta_k}) \geq I_{\min}$, it follows that $I(t + \tau_{\eta_k}) \geq I_{\min}e^{-b_{\max}t}$ for all $t > 0$. As a result, with $\sigma_{\eta_k+1} < T_3$, $I_{\eta_k+1} > \Delta := I_{\min}e^{-b_{\max}T_3}$.

Let $\delta_2 > 0$, we choose $\bar{T}_3 = T_1(\delta_2)$ as in Lemma 5.1.8 for the set $J = H_{\Delta}$. Because $I_{\eta_k} \geq \delta_1$, it follows $I_{\eta_k+1} \in H_{\Delta}$ and $(S_{\eta_k+2}, I_{\eta_k+2}) \in \mathcal{U}_{\delta_2}(s_*^+, i_*^+)$ provided $\sigma_{\eta_k+1} < T_3, \sigma_{\eta_k+2} > \bar{T}_3$. From (5.1.12) we see that $(S_{\eta_k+2}, I_{\eta_k+2}) \in \mathcal{U}_{\delta_2}(s_*^+, i_*^+)$ for infinitely many k . This means that $(s_*^+, i_*^+) \in \Omega(s_0, i_0, \omega)$ for almost all ω .

Next, we show that $\{\pi_t^-(s_*^+, i_*^+) : t \geq 0\} \subset \Omega(s_0, i_0, \omega)$ a.s. Consider a point $(\bar{s}, \bar{i}) = \pi_{\bar{T}_2}^-(s_*^+, i_*^+)$. By virtue of Lemma 5.1.10, for any $\delta_4 > 0$, there are δ_3, \bar{T}_2 such that if $(u, v) \in \mathcal{U}_{\delta_3}(s_*^+, i_*^+)$ then $\pi_t^-(u, v) \in \mathcal{U}_{\delta_4}(\bar{s}, \bar{i})$ for all $T_2 - \bar{T}_2 < t < T_2 + \bar{T}_2$. We now construct the sequence of stopping times

$$\begin{aligned}
\zeta_1 &= \inf\{2k+1 : (S_{2k+1}, I_{2k+1}) \in \mathcal{U}_{\delta_3}(s_*^+, i_*^+)\}, \\
\zeta_2 &= \inf\{2k+1 > \zeta_1 : (S_{2k+1}, I_{2k+1}) \in \mathcal{U}_{\delta_3}(s_*^+, i_*^+)\}, \\
&\dots \\
\zeta_n &= \inf\{2k+1 > \zeta_{n-1} : (S_{2k+1}, I_{2k+1}) \in \mathcal{U}_{\delta_3}(s_*^+, i_*^+)\} \dots
\end{aligned}$$

For $(s_*^+, i_*^+) \in \Omega(s_0, i_0, \omega)$, it follows that $\zeta_n < \infty$ and $\lim_{n \rightarrow \infty} \zeta_n = \infty$ a.s.. Since $\{\zeta_k = n\} \in \mathcal{F}_0^n$, $\{\zeta_k\}$ is independent of \mathcal{F}_n^∞ . Put

$$B_k = \{\sigma_{\zeta_k+1} \in [T_2 - \bar{T}_2, T_2 + \bar{T}_2]\}, \quad k = 1, 2, \dots$$

By the same argument as above we obtain $\mathbb{P}\{\omega : \sigma_{\zeta_n+1} \in [T_2 - \bar{T}_2, T_2 + \bar{T}_2] \text{ i.o. of } n\} = 1$. This implies $(S_{\zeta_k+1}, I_{\zeta_k+1}) \in \mathcal{U}_{\delta_4}(\bar{s}, \bar{i})$ for infinitely many times and $(\bar{s}, \bar{i}) \in \Omega(s_0, i_0, \omega)$ a.s. Thus, $\{\pi_t^-(s_*^+, i_*^+) : t \geq 0\} \subset \Omega(s_0, i_0, \omega)$.

Based on Lemmas 5.1.10, 5.1.11 and using a similar argument, we see that $\{\pi_{t_2}^+ \pi_{t_1}^-(s_*^+, i_*^+) : t_1 \geq 0, t_2 \geq 0\} \subset \Omega(s_0, i_0, \omega)$. By induction, we conclude $\Gamma \subset \Omega(s_0, i_0, \omega)$. Moreover, $\bar{\Gamma} \subset \Omega(s_0, i_0, \omega)$ since $\Omega(s_0, i_0, \omega)$ is a closed set. \square

Theorem 5.1.13. *Suppose $\lambda > 0$,*

a) *If*

$$\frac{a(+)}{a(-)} = \frac{b(+)}{b(-)} = \frac{c(+)}{c(-)}, \quad (5.1.13)$$

the systems (5.1.4) and (5.1.5) have the same equilibrium. Moreover, all positive solutions to the system (5.1.3) converge to this equilibrium with probability 1.

b) *If (5.1.13) is not satisfied then, with probability 1, the $\bar{\Gamma} = \Omega(s_0, i_0, \omega)$. Moreover, $\bar{\Gamma}$ absorbs all positive solutions in the sense that for any initial value $(s_0, i_0) \in \text{int}\mathbb{R}_+^2$, the value $\gamma(\omega) = \inf\{t > 0 : (S(\bar{t}, s_0, i_0, \omega), I(\bar{t}, s_0, i_0, \omega)) \in \bar{\Gamma} \forall \bar{t} > t\}$ is finite outside a \mathbb{P} -null set.*

Proof. a) It is easy to see that the systems (5.1.4) and (5.1.5) have the same equilibrium, $(s_*^+, i_*^+) = (s_*^-, i_*^-) =: (s_*, i_*)$ if and only if the condition (5.1.13) is satisfied. Let $\varepsilon > 0$ be arbitrary. Since (s_*, i_*) is globally asymptotically stable, there is a neighborhood $V_\varepsilon \subset \mathcal{U}_\varepsilon(s_*, i_*)$, invariant under the system (5.1.4) (see The Stable Manifold Theorem, [115, pp 107]). Under the condition (5.1.13), the vector fields of both systems (5.1.4) and (5.1.5) have the same direction at every point (s, i) . As a result, V_ε is also invariant under the system (5.1.5), which implies that V_ε is invariant under the system (5.1.3). By Theorem 5.1.12, $(s_*, i_*) \in \Omega(s_0, i_0, \omega)$ for almost all ω . Therefore, $T_{V_\varepsilon} = \inf\{t > 0 : (S(t), I(t)) \in V_\varepsilon\} < \infty$ a.s. Consequently, $(S(t), I(t)) \in V_\varepsilon \forall t > T_{V_\varepsilon}$. This property says that $(S(t), I(t))$ converges to (s_*, i_*) with probability 1 if $S(0) > 0, I(0) > 0$.

b) We will show that if there exists a $t_0 > 0$ such that the point $(\bar{s}_0, \bar{i}_0) = \pi_{t_0}^-(s_*^+, i_*^+)$ satisfies the following condition

$$\det \begin{pmatrix} \dot{S}^+(\bar{s}_0, \bar{i}_0) & \dot{S}^-(\bar{s}_0, \bar{i}_0) \\ \dot{I}^+(\bar{s}_0, \bar{i}_0) & \dot{I}^-(\bar{s}_0, \bar{i}_0) \end{pmatrix} \neq 0, \quad (5.1.14)$$

then, with probability 1, the closure $\bar{\Gamma}$ of Γ coincides $\Omega(s_0, i_0, \omega)$ and $\bar{\Gamma}$ absorbs all positive solutions.

Indeed, let $(\bar{s}_0, \bar{i}_0) = \pi_{t_0}^-(s_*^+, i_*^+)$ be a point in $\text{int}\mathbb{R}_+^2$ satisfying the condition (5.1.14). By the existence and continuous dependence on the initial values of the solutions, there exist two numbers $d > 0$ and $e > 0$ such that the function $\varphi(t_1, t_2) = \pi_{t_2}^+ \pi_{t_1}^-(\bar{s}_0, \bar{i}_0)$ is defined and continuously differentiable in $(-d, d) \times (-e, e)$. We note that

$$\det \left(\frac{\partial \varphi}{\partial t_1}, \frac{\partial \varphi}{\partial t_2} \right) \Big|_{(0,0)} = \det \begin{pmatrix} -a(+)\bar{s}_0\bar{i}_0 + c(+)(N - \bar{s}_0 - \bar{i}_0) & -a(-)\bar{s}_0\bar{i}_0 + c(-)(N - \bar{s}_0 - \bar{i}_0) \\ a(+)\bar{s}_0\bar{i}_0 - b(+)\bar{i}_0 & a(-)\bar{s}_0\bar{i}_0 - b(-)\bar{i}_0 \end{pmatrix} \neq 0.$$

Therefore, by the Inverse Function Theorem, there exist $0 < d_1 < d, 0 < e_1 < e$ such that $\varphi(t_1, t_2)$ is a diffeomorphism between $V = (0, d_1) \times (0, e_1)$ and $U = \varphi(V)$. As a

consequence, U is an open set. Moreover, for every $(s, i) \in U$, there exists a $(t_1^*, t_2^*) \in (0, d_1) \times (0, e_1)$ such that $(s, i) = \pi_{t_2^*}^+ \pi_{t_1^*}^-(\bar{s}_0, \bar{i}_0) \in S$. Hence, $U \subset \Gamma \subset \Omega(s_0, i_0, \omega)$. Thus, there is a stopping time $\gamma < \infty$ a.s. such that $(S(\gamma), I(\gamma)) \in U$. Since Γ is a forward invariant set and $U \subset \Gamma$, it follows that $(S(t), I(t)) \in \Gamma \forall t > \gamma$ with probability 1. The fact $(S(t), I(t)) \in \Gamma$ for all $t > \gamma$ implies that $\Omega(s_0, i_0, \omega) \subset \bar{\Gamma}$. By combining with Theorem 5.1.12 we get $\bar{\Gamma} = \Omega(s_0, i_0, \omega)$ a.s..

Moreover, we see that when condition (5.1.13) does not happen, it ensures the existence of t_0 satisfying (5.1.14). Indeed, consider the set of all $(s, i) \in \text{int } \mathbb{R}_+^2$ satisfying

$$\det \begin{pmatrix} \dot{S}^+(s, i) & \dot{S}^-(s, i) \\ \dot{I}^+(s, i) & \dot{I}^-(s, i) \end{pmatrix} = 0, \quad (5.1.15)$$

or

$$[-a(+)si+c(+)(N-s-i)][a(-)s-b(-)] - [-a(-)si+c(-)(N-s-i)][a(+)s-b(+)] = 0. \quad (5.1.16)$$

The equation (5.1.16) describes a quadratic curve (5.1.16). However, it is easy to prove that any quadratic curve is not the integral curve of the system (5.1.5). This means that we can find a t_0 such that the point $(\bar{s}_0, \bar{i}_0) = \pi_{t_0}^-(s_*^+, i_*^+)$ satisfies the condition (5.1.14). The proof is complete. \square

5.1.4 The semigroup and the stability in distribution

It is well-known that the pair $(\xi_t, S(t), I(t))$ is a homogeneous Markov process with the state space $\mathcal{V} := E \times \text{int } \mathbb{R}_+^2$. Let $\mathcal{B}(\mathcal{V})$ be the Borel σ -algebra on \mathcal{V} and λ be the Lebesgue measure on $\text{int } \mathbb{R}_+^2$. Denote by m the product measure on $(\mathcal{V}, \mathcal{B}(\mathcal{V}))$ defined by $m(+, A) = p\lambda(A)$ and $m(-, A) = q\lambda(A)$.

As shown in [51, Lemma 3.1], if the distribution of $(\xi_0, S(0), I(0))$ is absolutely continuous with respect to the measure m , so is the distribution of $(\xi_t, S(t), I(t))$. We can therefore define $P(t)f$ to be the density function of $(\xi_t, S(t), I(t))$ given that $(\xi_0, S(0), I(0))$ has the density f .

If $\lambda > 0$ and (5.1.13) holds, all positive solutions converge almost surely to the equilibrium $(s_*^+, i_*^+) = (s_*^-, i_*^-)$. Otherwise, we have

Theorem 5.1.14. *If $\lambda > 0$ and (5.1.13) does not hold, then $(\xi_t, S(t), I(t))$ has a stationary distribution ν^* , concentrated on $E \times (\nabla \cap \text{int } \mathbb{R}_+^2)$. In addition, ν^* is the unique stationary distribution having the density f^* , and $\lim_{t \rightarrow \infty} \|P(t)f - f^*\| = 0$ for any $f \in \mathcal{D}$.*

Proof. We firstly point out the existence of a stationary distribution of the process $(\xi_t, S(t), I(t))$. From the proof of Proposition 5.1.1, we have

$$\liminf_{t \rightarrow \infty} \frac{1}{t} \int_0^t I(\bar{t}) d\bar{t} \geq \frac{c_{\min}}{(a_{\max}N + c_{\max})a_{\max}} \lambda =: \rho > 0.$$

Denote by $\mathbf{1}_A$ the indicator function of the set A . By using the relations

$$\begin{aligned} \frac{1}{t} \int_0^t I(\bar{t}) d\bar{t} &= \frac{1}{t} \int_0^t I(\bar{t}) \mathbf{1}_{\{I(\bar{t}) < \frac{\rho}{2}\}} d\bar{t} + \frac{1}{t} \int_0^t I(\bar{t}) \mathbf{1}_{\{I(\bar{t}) \geq \frac{\rho}{2}\}} d\bar{t} \\ &\leq \frac{\rho}{2} + \frac{N}{t} \int_0^t \mathbf{1}_{\{I(\bar{t}) \geq \frac{\rho}{2}\}} d\bar{t}, \end{aligned}$$

it follows, with probability 1, that

$$\liminf_{t \rightarrow \infty} \frac{1}{t} \int_0^t \mathbf{1}_{\{I(\bar{t}) \geq \frac{\rho}{2}\}} d\bar{t} \geq \frac{\rho}{2N}.$$

Applying Fatou lemma yields

$$\liminf_{t \rightarrow \infty} \frac{1}{t} \int_0^t \mathbb{P}\{I(\bar{t}) \geq \frac{\rho}{2}\} d\bar{t} \geq \frac{\rho}{2N}. \quad (5.1.17)$$

Consider the process $(\xi_t, S(t), I(t))$ on a larger state space $E \times (\nabla \setminus \{(s, i) : s = 0, 0 \leq i \leq N\})$. It is easy to prove that $(\xi_t, S(t), I(t))$ is a Feller process. Therefore, by using [102, Theorem 4.5] (or [134]) the above estimate (5.1.17) implies the existence of an invariant probability measure ν for the process $(\xi_t, S(t), I(t))$ on $E \times (\nabla \setminus \{(s, i) : s = 0, 0 \leq i \leq N\})$. Since $\{(s, i) : i = 0, 0 \leq s \leq N\}$ is invariant and $\lim_{t \rightarrow \infty} I(t) = 0$ if $S(0) = 0$, it follows that $\nu(\{(s, i) : i = 0, 0 \leq s \leq N\}) = 0$. Thus, $\nu(E \times (\nabla \cap \text{int}\mathbb{R}_+^2)) > 0$. By virtue of invariant property of $E \times \text{int}\mathbb{R}_+^2$, the measure ν^* defined by $\nu^*(A) = \frac{\nu(A \cap E \times (\nabla \cap \text{int}\mathbb{R}_+^2))}{\nu(E \times (\nabla \cap \text{int}\mathbb{R}_+^2))}$ for any measurable $A \in \mathcal{B}(\mathcal{V})$ is a stationary distribution on $E \times (\nabla \cap \text{int}\mathbb{R}_+^2)$ of the process $(\xi_t, S(t), I(t))$.

The asymptotic stability of f^* can be proved by using (5.1.14); the arguments analogous to [51, Proposition 3.1] and then applying [118, Proposition 2]. The proof is complete. \square

5.1.5 Simulation and discussion

We illustrate the above model by following numerical examples.

Example I: $\lambda > 0$ and the endemic is present in both states (see figure 5.6). It corresponds to $\alpha = 15, \beta = 18, a(+) = 1.2, b(+) = 432, c(+) = 265, a(-) = 1.5, b(-) = 139, c(-) = 428, N = 500$, the initial condition $(S(0), I(0)) = (250, 10)$ and number of switches $n = 500$. In this example, $\lambda \approx 369.36$, the solution of (5.1.3) switches between two asymptotically stable positive equilibria of the systems (5.1.4) and (5.1.5).

Example II: $\lambda > 0$ and one state is endemic, the other is disease free. The system (5.1.4) with coefficients $a(+) = 1.6, b(+) = 169, c(+) = 486$ has a asymptotically stable positive equilibrium and the system (5.1.5) with coefficients $a(-) = 0.7, b(-) = 375, c(-) = 328$ tends to the quantity of population $N = 500$,

the number of switches $n = 700$, transition intensities $\alpha = 8\beta = 15$ and initial condition $(S(0), I(0)) = (104, 336)$. Since $\lambda \approx 402.83$, the system (5.1.3) is persistent (see figure 5.9).

Example III: $\lambda < 0$ and a system has positive equilibrium, the other has disease free equilibrium (figure 5.12). The parameters of the model are $\alpha = 20, \beta = 5, a(+) = 1.9, b(+) = 176, c(+) = 465, a(-) = 0.5, b(-) = 455, c(-) = 347, N = 500, (S(0), I(0)) = (64, 362), n = 100$. Although the positive equilibrium of the system (5.1.4) is asymptotically stable, the system (5.1.3) is not persistent because $\lambda = -9.2$.

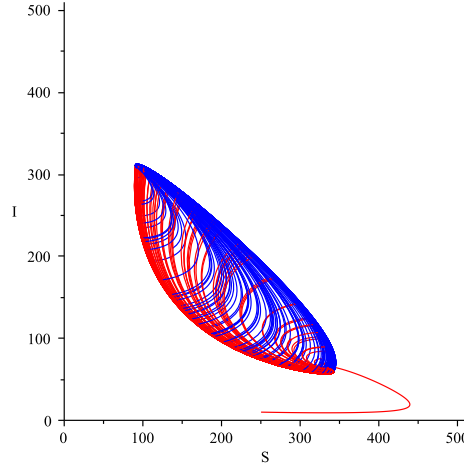


Figure 5.6: Orbit of the system (5.1.3) in example I.

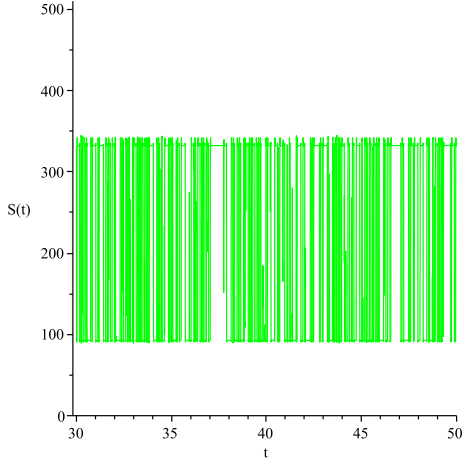


Figure 5.7: Trajectory $S(t)$ in example I

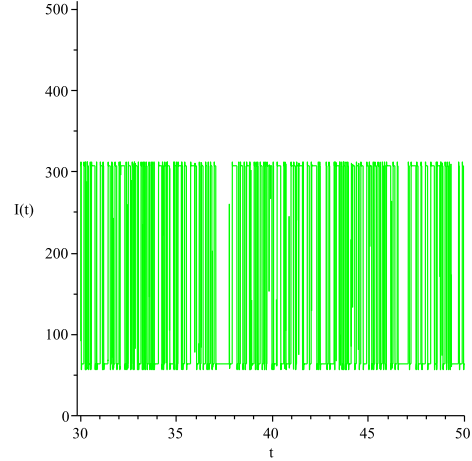


Figure 5.8: Trajectory $I(t)$ in example I.

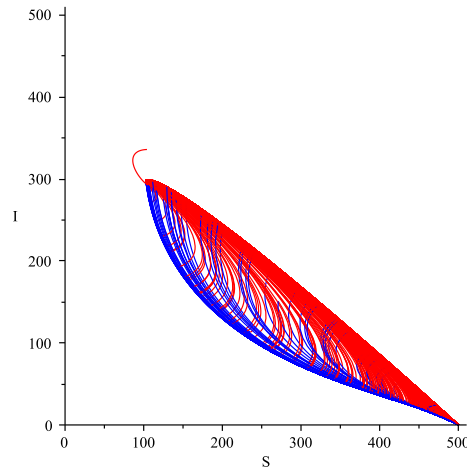
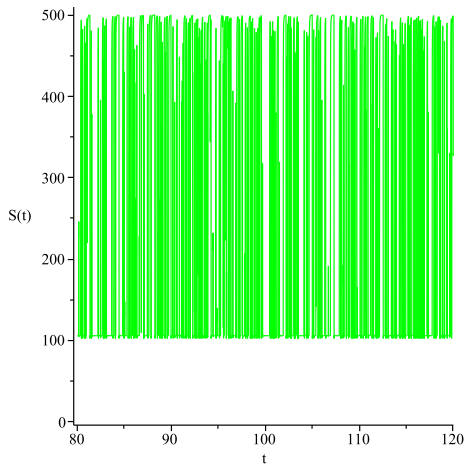
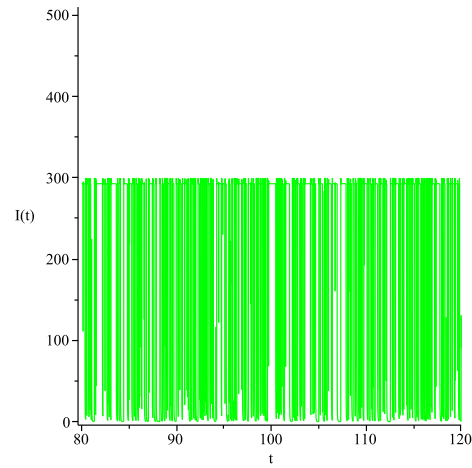


Figure 5.9: Orbit of the system (5.1.3) in example II.

Figure 5.10: Trajectory $S(t)$ in example IIFigure 5.11: Trajectory $I(t)$ in example II.

The basic reproduction number \mathcal{R}_0 is an important concept in epidemiology. \mathcal{R}_0 is the threshold parameter for many epidemiological models, it informs whether the disease becomes extinct or whether the disease is endemic. For example, there are many recent papers about periodic epidemic models that concentrate on defining and computing \mathcal{R}_0 (see [17], [18], [55], [144] [151]). In the classic SIRS model (5.1.1), \mathcal{R}_0 is valued by ratio $\frac{Na}{b}$, it represents the rate of increase of new infections generated by a single infectious individual in a total sane population. Based on this \mathcal{R}_0 , we give out the key parameter λ for our stochastic SIRS model. λ reads as follows:

$$\lambda = p(a(+)N - b(+)) + q(a(-)N - b(-)).$$

This is the average of two terms associated with each system $+$ or $-$ weighted by the switching intensities. Therefore, in the stochastic model, λ can be interpreted as the

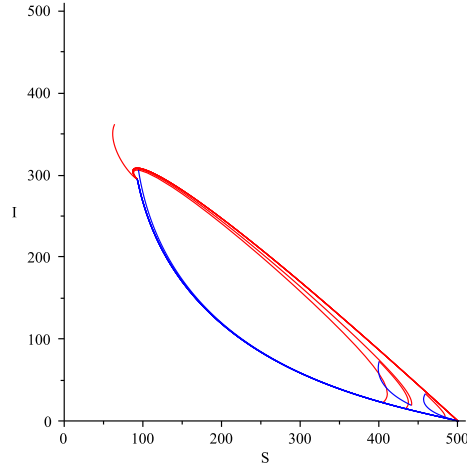
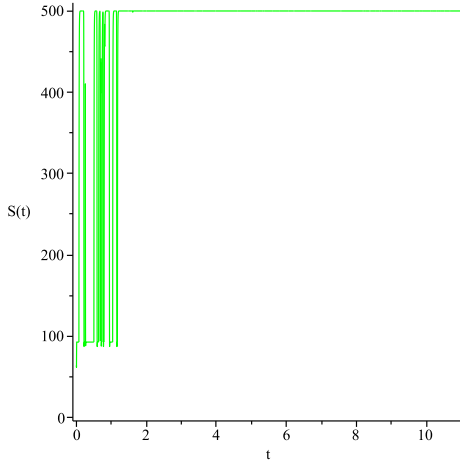
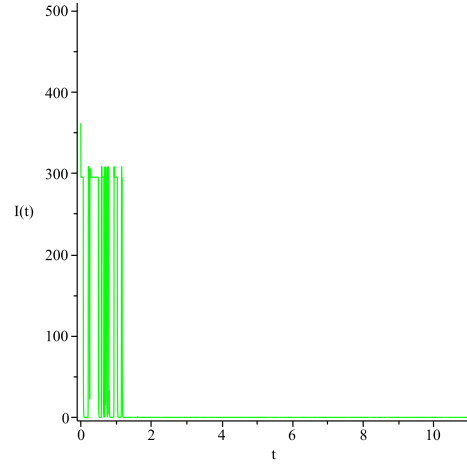


Figure 5.12: Orbit of the system (5.1.3) in example III.

Figure 5.13: Trajectory $S(t)$ in example IIIFigure 5.14: Trajectory $I(t)$ in example III.

average number of infective individuals generated by a single infectious individual in a totally sane population for the total system with random switches. We can, therefore, understand that when λ is positive, it signifies that asymptotically the total system will go towards an endemic state while the disease will vanish provided that it is negative. Hence, for the stochastic model, λ is a very important parameter that enables us to obtain important informations about the asymptotic behavior of the total system.

We illustrate different situations in the following numerical simulations. Examples I and II show cases where λ is positive, the first one illustrates the switching between two endemic systems $+$ and $-$, whilst the second one depicts a system composed of an endemic case $+$ and a case $-$ for which the disease free equilibrium is stable. In both examples, the simulations show that asymptotically the total system

persists leading to an endemic situation.

The last example III considers the case of $\lambda < 0$, with an endemic system + and for the other one – a stable disease free equilibrium. As expected, the simulation shows that after several switches, the disease is globally eradicated.

Examples II and III are interesting because they illustrate a similar case, i.e. when systems + and – have opposite trends, system + being endemic and system – being disease free. In those examples, it is thus questionable to predict what will be the global evolution of the complete system switching at random between these two different situations. The answer is given by looking at the sign of parameter λ which allow us to predict if the disease will globally invade or vanish in the long term.

Global changes may have important consequences on the spreading of emergent diseases and epidemics. Therefore, it is important to provide pertinent tools that allow us to make suitable predictions about the possibility of emergence of a disease in a changing environment undergoing climatic and environmental changes. The aim of this chapter was to provide such efficient tools.

As a perspective, the system would be extended to the case of a system switching randomly between n states, $n > 2$. It would also be interesting to test the model on real situations, like malaria, switching between wet and dry periods. Otherwise, for further study on the epidemic models under the effect of random environmental conditions, we could add some more other stochastic factors as in [26] to this SIRS model.

5.2 Evolution of Lotka-Volterra predator-prey systems under telegraph noise

5.2.1 Model

The dynamics of predator-prey systems have been investigated very largely in the frame of deterministic models, Edelstein-Keshet (1998) [52], Murray (2002) [105]. In Bazykin (1998) [22], one can find a review of most classical deterministic predator-prey models. The two variables are the prey $x(t)$ and predator $y(t)$ densities at time t . The classical form of a predator-prey model is the following one:

$$\begin{cases} \frac{dx}{dt} = f(x) - h(x, y)y \\ \frac{dy}{dt} = \tilde{e}h(x, y)y - \mu y, \end{cases}$$

where the function $f(x)$ is the natural growth function of the prey, $h(x, y)y$ is the capture term; \tilde{e} is a positive prey biomass into predator biomass conversion parameter. μ is the natural mortality rate for predators. $h(x, y)$ is the so-called functional response, i.e., the prey density captured per unit of time and per unit of predator density. In the classical Lotka-Volterra model, it is assumed that the functional response is type I, i.e., depending only on the prey density and linear, i.e., $h(x) = qx$

where q is a positive constant which is called the catch-ability. It is also usual to assume that prey grows logistically leading to the model:

$$\begin{cases} \frac{dx}{dt} = x \left(r \left(1 - \frac{x}{K} \right) - qy \right) = x (a - bx - cy) \\ \frac{dy}{dt} = (\tilde{e}qx - \mu) y = (-d + ex) y. \end{cases}$$

Where r is the growth rate of the prey and K its carrying capacity. For the sake of simplification, in the next sections, we use the model under the form involving the parameter set (a, b, c, d, e) and the links with ecological parameters $(r, K, q, \mu, \tilde{e})$ is not given here because it is obvious.

This classical Lotka-Volterra model assumes that species live in a constant environment. However, it is clear that it is not the case in reality and that it is important to take into account the variability of the environment which may have important consequences on the dynamics and persistence of a predator-prey community. The variability of the environment may be expressed under the stochastic factors. For the stochastic Lotka-Volterra equation, there is not too much in mathematical literature, and almost nothing in statistical inference. Here, we mention one of the first attempts in this direction, the very interesting paper of Arnold et al. [7] in which the authors used the theory of Brownian motion processes and the related white noise models to study the sample paths of the equation. For the branching models in a varying environment, we can refer to [2, 3, 127]. A systematic review has been given in [1]. In the simplest case, one might consider that environmental conditions can switch between two states, a hot and cold one, a dry state and wet one. Thus, we can suppose there is a telegraph noise affecting on the model in the form of switching between two-element set, $\mathbb{E} = \{1, 2\}$. With different states, the coefficients of model are different. The stochastic displacement of environmental conditions provokes model to change from the system in state one to the system in state two and vice versa.

Let's consider again process (ξ_t) mentioned in section 5.1.2. $(\xi_t)_{t \geq 0}$ is a Markov process, defined on the probability space $(\Omega, \mathcal{F}, \mathbb{P})$, taking values in the set of two elements, say $\mathbb{E} = \{1, 2\}$. (ξ_t) has the transition intensities $1 \xrightarrow{\alpha} 2$ and $2 \xrightarrow{\beta} 1$ with $\alpha > 0, \beta > 0$. The process (ξ_t) has a unique stationary distribution

$$p = \lim_{t \rightarrow \infty} \mathbb{P}\{\xi_t = 1\} = \frac{\beta}{\alpha + \beta}; \quad q = \lim_{t \rightarrow \infty} \mathbb{P}\{\xi_t = 2\} = \frac{\alpha}{\alpha + \beta}.$$

Lotka-Volterra predator-prey system with telegraph noise (ξ_t) is described by equation

$$\begin{cases} \dot{x} = x (a(\xi_t) - b(\xi_t)x - c(\xi_t)y), \\ \dot{y} = y (-d(\xi_t) + e(\xi_t)x), \end{cases} \quad (5.2.1)$$

where $g : \mathbb{E} \rightarrow (0, \infty)$ for $g = a, b, c, d, e$.

This section studies the dynamical behavior of system under telegraph noise. It is structured into four subsections. In subsection 5.2.2, we summarize our paper [12]. Paper [12] presents this model with carrying capacity of environment ($K < \infty$ i.e. $b \neq 0$) where the dynamics of the system is quite different. The predator may be

extinct when one deterministic system has only non positive rest point. However, if two deterministic systems have positive rest points, it is proved that the model will be permanent with probability 1. Moreover, we show the existence of stationary distribution of solution in this case. When the carrying capacity of environment is absent ($K = \infty$ i.e. $b = 0$), the telegraph noise does the model chaotically. It can not be permanent if the positive rest points of two deterministic systems do not coincide [138]. This case is shown in our paper [138] and summarized in subsection 5.2.3. Last subsection is discussion and conclusion.

5.2.2 Predator-prey system with carrying capacity

The following subsection presents main results of paper [12]. We consider Lotka-Volterra predator-prey system (5.2.1) in case $b(\xi_t) \neq 0$

$$\begin{cases} \dot{x} = x(a(\xi_t) - b(\xi_t)x - c(\xi_t)y), \\ \dot{y} = y(-d(\xi_t) + e(\xi_t)x), \end{cases} \quad (5.2.2)$$

where $g : \mathbb{E} \rightarrow (0, \infty)$ for $g = a, b, c, d, e$. The noise (ξ_t) intervenes virtually into the equation (5.2.2), it makes a switching between the deterministic system

$$\begin{cases} \dot{x}_1(t) = x_1(t)(a_1 - b_1x_1(t) - c_1y_1(t)), \\ \dot{y}_1(t) = y_1(t)(-d_1 + e_1x_1(t)), \end{cases} \quad (5.2.3)$$

and the deterministic one

$$\begin{cases} \dot{x}_2(t) = x_2(t)(a_2 - b_2x_2(t) - c_2y_2(t)), \\ \dot{y}_2(t) = y_2(t)(-d_2 + e_2x_2(t)), \end{cases} \quad (5.2.4)$$

where $g_i = g(i)$ for $i = 1, 2$ and $g = a, b, c, d, e$.

It is well-known that the systems (5.2.3) and (5.2.4) respectively have the rest points

$$x_i^* = \frac{d_i}{e_i}, \quad y_i^* = \frac{a_ie_i - b_id_i}{c_ie_i}, \quad i = 1, 2, \quad (5.2.5)$$

and their global dynamics depend on these rest points (see [22]). Concretely, if $y_i^* > 0$ then the i^{th} -rest point is asymptotically stable, i.e., $\lim_{t \rightarrow \infty} (x_i(t), y_i(t)) = (x_i^*, y_i^*)$ when $x_i(0) > 0, y_i(0) > 0$. If $y_i^* \leq 0$ then $\lim_{t \rightarrow \infty} (x_i(t), y_i(t)) = (\frac{a_i}{b_i}, 0)$ for $i = 1, 2$.

The behavior of two boundary equations is easy to be studied. In the case where the prey is absent, the quantity $v(t)$ of predator at the time t satisfies the equation $\dot{v} = -d(\xi_t)v$. Thus, $v(t)$ decreases exponentially to 0. Similarly, without the predator, the quantity $u(t)$ of the prey at the time t satisfies the logistic equation

$$\dot{u} = u(a(\xi_t) - b(\xi_t)u), \quad u(0) > 0. \quad (5.2.6)$$

Let $(x_0, y_0) \in \mathbb{R}_+^2$. Denote by $(x(t, x_0, y_0), y(t, x_0, y_0))$ the solution of (5.2.2) satisfying the initial condition $(x(0, x_0, y_0), y(0, x_0, y_0)) = (x_0, y_0)$. For the sake of simplification, we write $(x(t), y(t))$ for $(x(t, x_0, y_0), y(t, x_0, y_0))$. The following propositions will give the conditions for the persistence of system (5.2.2)

Proposition 5.2.1. *There exists a positive number x_{\min} , independent from the choice of $(x_0, y_0) \in \mathbb{R}_+^2$, such that $x(t)$ is ultimately bounded below by x_{\min} . This means that there is $t_0 > 0$ such that $x(t) \geq x_{\min}$ for all $t \geq t_0$.*

Denote

$$\lambda := \int_I (p(-d_1 + e_1 u) \mu_1(u) + q(-d_2 + e_2 u) \mu_2(u)) du. \quad (5.2.7)$$

Proposition 5.2.2.

- a) *If $\lambda > 0$ then there is a positive number δ such that $\limsup_{t \rightarrow \infty} y(t, x_0, y_0) > \delta$ with probability 1.*
- b) *If $\lambda < 0$ we have $\lim_{t \rightarrow \infty} y(t, x_0, y_0) = 0$ with probability 1.*

By combining the propositions 5.2.1 and 5.2.2 we have corollary

Corollary 5.2.3. *If $\lambda > 0$ then (5.2.2) is persistent with probability 1.*

Let $\omega(x_0, y_0)$ be the ω -limit set of the solution $(x(t, x_0, y_0), y(t, x_0, y_0))$ of the system (5.2.2). We have

Theorem 5.2.4.

- a) *Suppose that $\lambda > 0$*

1. *If $y_1^* > 0$ and $y_2^* > 0$, both the positive orbit γ_1 of the solution $(x_1(t, x_2^*, y_2^*), y_1(t, x_2^*, y_2^*))$ of the system (5.2.3) and γ_2 of the solution $(x_2(t, x_1^*, y_1^*), y_2(t, x_1^*, y_1^*))$ of system (5.2.4) are subsets of $\omega(x_0, y_0)$. Moreover,*
2. *Any positive orbit $\bar{\gamma}_2$ of the solution $(x_2(t, \bar{x}, \bar{y}), y_2(t, \bar{x}, \bar{y}))$ of the system (5.2.4), starting in a point $(\bar{x}, \bar{y}) \in \gamma_1$ at $t = 0$, is a subset of $\omega(x_0, y_0)$. Similarly, any positive orbit $\bar{\gamma}_1$ of the solution $(x_1(t, \bar{x}, \bar{y}), y_1(t, \bar{x}, \bar{y}))$ of the system (5.2.3), starting in a point $(\bar{x}, \bar{y}) \in \gamma_2$ at $t = 0$, is a subset of $\omega(x_0, y_0)$.*
3. *If $y_1^* > 0$ and $y_2^* < 0$, then we have a similar result as in 1.; provided that (x_2^*, y_2^*) is replaced by $(\frac{a_2}{b_2}, 0)$ and γ_1 is replaced by closure of $\bar{\gamma}_1$ - says $\hat{\gamma}_1$. Concurrently, $\gamma^u \subset \omega(x_0, y_0)$ with γ^u to be the ω -limit set of $(u(t), 0)$, here $u(t)$ is the solution of the system (5.2.6).*

- b) *If $\lambda < 0$, $y_1^* < 0$ and $y_2^* < 0$ then $\gamma^u \equiv \omega(x_0, y_0)$.*

Theorem 5.2.4 describes the subsets of ω -limit set of solution for each case. It is shown that the ω -limit sets include every orbit starting at a point on the curves linking two rest points of the subsystems.

The last theorem proves the existence of invariant measures

Theorem 5.2.5. *If $y_1^* > 0, y_2^* > 0, \lambda > 0$, the system (5.2.2) is permanent. Moreover, for the Markov process $(x(t), y(t), \xi_t)_{t \geq 0}$, there exists a stationary distribution.*

Next, we present some numerical simulations. As the first example, we consider the case $a_1 = 4.2, b_1 = 1, c_1 = 1.1, d_1 = 5, e_1 = 1.8, a_2 = 6, b_2 = 0.8, c_2 = 1.3, d_2 = 9.4, e_2 = 2.5, x(0) = 4, y(0) = 4.3, \alpha = 0.6, \beta = 0.8$, where $y_1^* > 0, y_2^* > 0$. The number of switching is $n = 300$. The individual sample paths in the figure 5.15 illustrate the ω -limit set in the theorem 5.2.4. The figure 5.16 shows the oscillations of the population sizes $x(t)$ and $y(t)$.

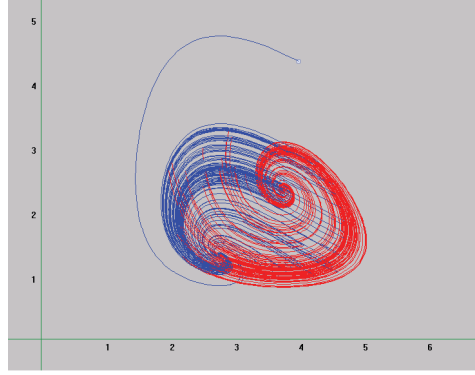


Figure 5.15: Orbit of system in case $y_1^* > 0, y_2^* > 0$. The solution moves between the two rest points $(2.77, 1.29)$ and $(3.76, 2.30)$ as switching occurs.

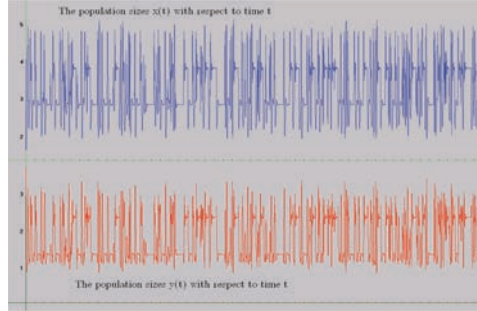


Figure 5.16: The oscillations of $x(t)$ and $y(t)$ in case $y_1^* > 0, y_2^* > 0$.

The next examples concern with the numerical solutions of systems where $y_1^* > 0, y_2^* < 0$. On the case *A* of the figure 5.17, we compute with $a_1 = 7.2, b_1 = 2.1, c_1 = 0.8, d_1 = 3.2, e_1 = 1.6, a_2 = 6.3, b_2 = 1.1, c_2 = 2.5, d_2 = 5.8, e_2 = 0.9, x(0) = 0.8, y(0) = 3.3, \alpha = 0.5, \beta = 0.4$ and the number of switching $n=500$. In this case $\lambda \approx 0.66 > 0$. As is seen $\limsup_{t \rightarrow \infty} y(t) > 0$ but $\liminf_{t \rightarrow \infty} y(t) = 0$.

For the case *B*, the parameters are $a_1 = 4.2, b_1 = 0.9, c_1 = 0.4, d_1 = 6.5, e_1 = 1.8, a_2 = 5.8, b_2 = 2, c_2 = 1.5, d_2 = 7.3, e_2 = 1.1, x(0) = 4.5, y(0) = 2.6, \alpha = 0.3, \beta = 0.6$, number of switching $n = 300$. Since $\lambda \approx -0.1 < 0$, it is seen that $\lim_{t \rightarrow \infty} y(t) = 0$ (according to the proposition 5.2.2). Thus the ω -limit set of all solutions starting in $\text{int } \mathbb{R}_+^2$ is the segment $[(4.7, 0); (2.9, 0)]$ (see the theorem 5.2.4).

We sketch the oscillations of $x(t)$ and $y(t)$ in these cases in the figure 5.18 and 5.19.

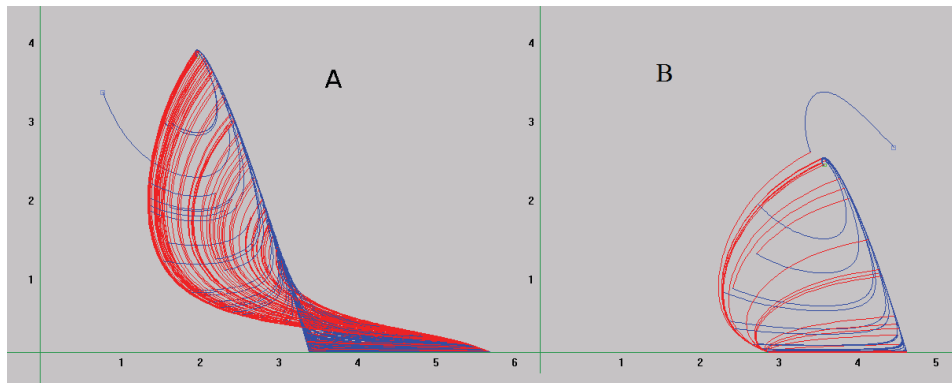


Figure 5.17: Orbit of system in case $y_1^* > 0, y_2^* < 0$.

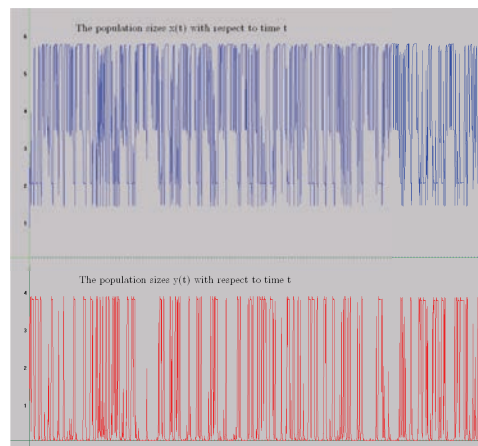


Figure 5.18: The oscillations of $x(t)$ and $y(t)$ in case A.

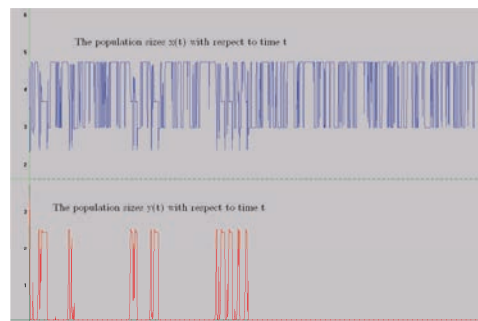


Figure 5.19: The oscillations of $x(t)$ and $y(t)$ in case B.

5.2.3 Predator-prey system with the absence of carrying capacity

This subsection is summarization of paper [138]. We study Lotka-Volterra predator-prey system (5.2.1) in case $b(\xi_t) = 0$

$$\begin{cases} \dot{x} = x(a(\xi_t) - c(\xi_t)y), \\ \dot{y} = y(-d(\xi_t) + e(\xi_t)x), \end{cases} \quad (5.2.8)$$

where $g : \mathbb{E} \rightarrow \mathbb{R}_+ \setminus \{0\}$ for $g = a, c, d, e$. In the case where the noise (ξ_t) intervenes virtually into Equation (5.2.8), it makes a switching between the deterministic system

$$\begin{cases} \dot{x}_1(t) = x_1(t)(a_1 - c_1 y_1(t)), \\ \dot{y}_1(t) = y_1(t)(-d_1 + e_1 x_1(t)), \end{cases} \quad (5.2.9)$$

and a deterministic one

$$\begin{cases} \dot{x}_2(t) = x_2(t)(a_2 - c_2 y_2(t)), \\ \dot{y}_2(t) = y_2(t)(-d_2 + e_2 x_2(t)). \end{cases} \quad (5.2.10)$$

[105] and [137] show that system (5.2.9) (resp. (5.2.10)) has a rest point $(x_1^*, y_1^*) = (\frac{a_1}{c_1}, \frac{d_1}{e_1})$ (resp. $(x_2^*, y_2^*) = (\frac{a_2}{c_2}, \frac{d_2}{e_2})$) and its solutions are periodic orbits.

Theorem 5.2.6. *Suppose that (5.2.9) and (5.2.10) have different rest points. For any initial point $(x_0, y_0) \in \text{int}\mathbb{R}_+^2$, we have with probability 1,*

$$\begin{aligned} \limsup_{t \rightarrow \infty} x(t, x_0, y_0) &= \infty, \liminf_{t \rightarrow \infty} x(t, x_0, y_0) = 0, \\ \limsup_{t \rightarrow \infty} y(t, x_0, y_0) &= \infty, \liminf_{t \rightarrow \infty} y(t, x_0, y_0) = 0. \end{aligned}$$

Theorem 5.2.7. *Suppose that (5.2.9) and (5.2.10) have a common rest point. For any initial point $(x_0, y_0) \in \text{int}\mathbb{R}_+^2$, we have with probability 1, either*

$$\lim_{t \rightarrow \infty} (x(t, x_0, y_0), y(t, x_0, y_0)) = (x_1^*, y_1^*) = (x_2^*, y_2^*), \quad (5.2.11)$$

or,

$$\limsup_{t \rightarrow \infty} x(t, x_0, y_0) = \infty, \liminf_{t \rightarrow \infty} x(t, x_0, y_0) = 0, \quad (5.2.12)$$

$$\limsup_{t \rightarrow \infty} y(t, x_0, y_0) = \infty, \liminf_{t \rightarrow \infty} y(t, x_0, y_0) = 0. \quad (5.2.13)$$

Theorem 5.2.6 and 5.2.7 mean that if the rest points of two systems do not coincide, all trajectories of the system perturbed by telegraph noise always leave from any compact set in $\text{int}\mathbb{R}_+^2$. In case two systems have the rest point in common, either the trajectory of a random predator-prey system converges to the common rest point or it leaves from any rectangle in $\text{int}\mathbb{R}_+^2$. These properties imply that such a system is neither permanent nor dissipative.

We illustrate our result by simulations. Figure 5.20 and 5.21 shows the behavior of the trajectory of the systems (5.2.8).

Case A corresponds to $a(1) = 2, b(1) = 2, c(1) = 3, d(1) = 2$ and $a(2) = 3, b(2) = 3, c(2) = 6, d(2) = 4$ with the initial condition $(2, 1.5)$. In this case, two systems have the rest point in common, the solution of (5.2.8) turns around the rest point for a while, and then leaves from any compact set.

Case B is related to $a(1) = 2, b(1) = 1, c(1) = 6, d(1) = 3$ and $a(2) = 2, b(2) = 2, c(2) = 3, d(2) = 2$, the initial condition is $(1, 2)$. In this case, two rest points are different, the solution leaves quickly from any compact set.

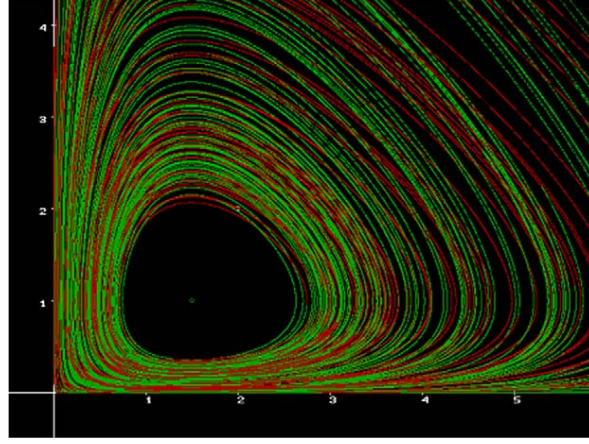


Figure 5.20: Orbits of system (5.2.8) for Case A

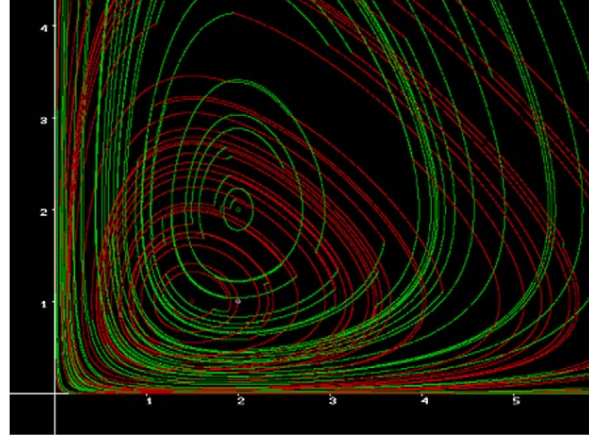


Figure 5.21: Orbits of system (5.2.8) for Case B

In both cases, the green line shows the trajectory of (5.2.8) subjected to System (5.2.9) and the red line shows the trajectory of (5.2.8) subjected to System (5.2.10).

Figure 5.22 (or 5.23) shows the time evolution of $x(t)$ and $y(t)$ corresponding to Case A (or B), respectively.

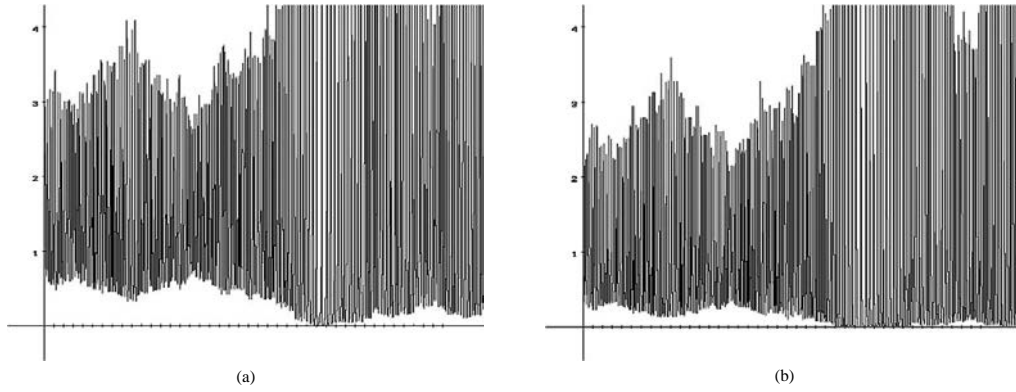


Figure 5.22: (a) Time evolution of $x(t)$ for Case A. (b) Time evolution of $y(t)$ for Case A

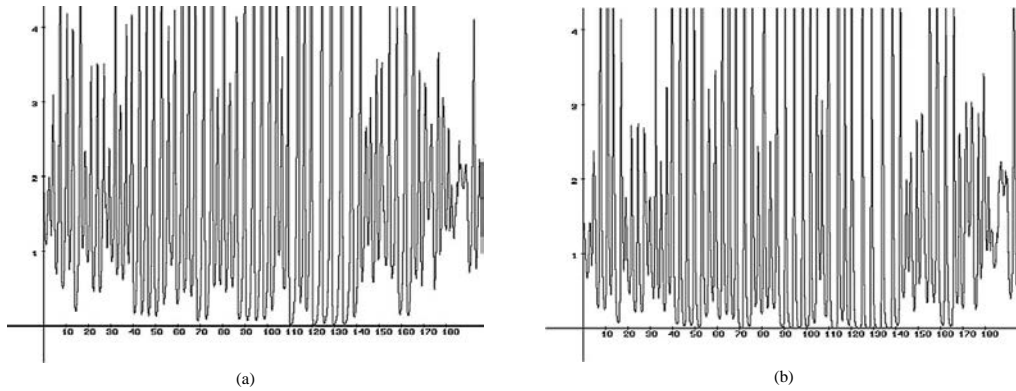


Figure 5.23: (a) Time evolution of $x(t)$ for Case B. (b) Time evolution of $y(t)$ for Case B

Remark 5.2.8. By simulation results, we observe that (5.2.11) does not occur. However, so far we are unable to prove this conjecture. This is still an open problem.

5.2.4 Discussion and conclusion

Up to now there have been proposed various dynamical models in ecology under the environmental fluctuations corresponding to seasonality. The deterministic switching between two different predator-prey systems exhibits more complex dynamics including stable equilibrium point, limit cycle, and also chaos [65]. The possibilities or the conditions for the coexistence of temporally segregated competitors in a cyclic environment [87] or two competing species following Lotka-Volterra competition system in a seasonally fluctuating environment [96] are studied. The stochastic change of environment gives the similar effect on population dynamics with seasonality [40]. Most of such models are formulated by deterministic dynamics, but some kind of stochasticity reflecting complexity of biological or environmental factors should be introduced in population dynamics. Slatkin [131] introduced

and analyzed a class of general models of single population which grows under the telegraph noise exactly same in this paper. In section 5.2 we obtained the results for two-species Lotka-Volterra predator-prey systems under telegraph noises. We believe the necessity to collect the results for various types of two-species dynamical systems, and to proceed to obtain the general conditions for the behaviors of the systems.

In subsection 5.2.2 we consider an ecology system where there are two species related by predator-prey relation and environment has a finite carrying capacity. The mathematical analysis presented in this model shows that according to the value of some number λ , one can make suitable predictions about the asymptotic behavior of the overall predator-prey system. Suppose that the evolution of every species depends on the quantity of rainfall for every period. If the rainfall is sufficient (good state), the catch ability of the predator is good and the quantity of every species asymptotes to the positive values (the prey and predator co-exist). Whenever the rainfall is small (bad state), the hunting potential of the predator becomes very weak and the amount of predator gets smaller with increasing of time (the predator vanishes). Suppose that the rainfall is in a stationary regime (switching stationarily between dry season and rainfall one). If the two states are good, i.e., both $y_1^* > 0$ and $y_2^* > 0$, although the quantity of two species is chaotic, but the system is still permanent. Consequently, none of species is extinct. When there is at least a system having the bad state, i.e., either $y_1^* < 0$ or $y_2^* < 0$ we see that $\liminf_{t \rightarrow \infty} y(t) = 0$. Depending on the sign of the value λ , the quantity of the predator $y(t)$ can be recovered or not. In case $\lambda > 0$ we have $\limsup_{t \rightarrow \infty} y(t) > 0$, i.e., the amount of the predator is recovered (of course in the rainfall season). If $\lambda < 0$ we have $\lim_{t \rightarrow \infty} y(t) = 0$, i.e., the predator vanishes.

The model of predator-prey with the absence of carrying capacity is studied in subsection 5.2.3. We obtain an interesting result. In the deterministic environment, this model has periodic solutions and two species are permanent. However, with the effect of the random switching of environment, the orbits of predator-prey model are very chaos and could be not permanent.

In view of practice, when the amount of a species is smaller than a threshold, we consider this species disappears in our system. The obtained results tell us that although the environment condition changes constantly (since the Markov switching process is stationary), species may vanish from ecology system. This warns us to have a timely decision to protect species in our ecology system.

Chapter 6

Conclusion

In this thesis we consider some ecosystem models. We try to show the dynamical behavior and the condition for existence of these models. The obtained results could be useful to explain some phenomena and give us some recommendations for the ecosystems.

Intraguild predation (IGP) occurs when one species prey upon another species with which it competes for a shared resource. IGP is common in nature, for examples lion and lynx, wolf and coyote, insects and arachnids, shark and other predator in marine ecosystems... In chapter 2 we study the effects of spatial heterogeneous environment and fast migration of individuals on coexistence of the IGP dynamics. We concentrate on a two-patch model including two species with IGP interaction. The interaction of two species is competition in one patch and in the other patch it is predation. We also assume two species are not coexistence in each patch. However, we have a interesting results that by the heterogeneous environment and fast migration between two patch, two species can be coexistence in some situation. In addition we are also interested in the effects of the migration parameters, the competition parameters and the predation ones on this coexistence. In fact, the shared resource of two species is hidden in this model. Hence, to describe IGP interaction in more detail, in a further work we will investigate a model with three species where two species have IGP interaction and they prey upon the third species. In the other hand, we can change functional response of predation to other type. We hope the model will have limit cycle if functional response is Holling type 2.

Chapter 3 presents a mathematical model of a fishery targeting a small pelagic fish population distributed over two sites, a marine protected area (MPA) and a fishing area where the fish population can be captured by purse-seine fishing boats. An aggregated model is obtained from complete model by using aggregation methods. Hence we describe the condition for the stableness of aggregation model and show that there is a proportion of small clusters which is maximum in terms of total catch on the long term for a given fishery and fishing effort. These results should allow adaptive management measures not only for the maintenance of model but also for the maximum of total catch. In this model we only investigate the effects of fish clustering on the total catch of a small pelagic purse seine fishery. In future

work, we will study the effects of both proportion of small cluster and proportion of MPA on this catch, then it can propose a suitable MPA.

In chapter 4 we study the dynamical relationship between three species in a nonautonomous model of one prey and two predators, in which the functional responses are of the form Beddington-DeAngelis functional response. We consider the model with general coefficients and periodic coefficients. The results show us when the model has globally asymptotically stable solution and the condition for the coexistence or extinction of species.

Randomness or stochasticity play a vital role in the dynamics of an ecological system and the variation of random factors can cause sharp changes in it. Chapter 5 shows some ecosystem models under random environment. This random factor is described by telegraph noise and it can do the models chaotically. We try to show the dynamics, persistence and permanence of the models. In some conditions, the models is persistent, permanent or not. The persistence is “not good” for epidemic model, it means the disease will globally invade in the long term. However, the permanence is “good” for predator-prey models, it ensures the species coexistence. We only investigate the models with the effect of telegraph noise in this chapter, then, for future work we can mention seasonality of environment characteristics to describe the models in more detail. How will the dynamical behavior of the models be if they have more than the two states of environment or if they have the fast migration of individuals as in chapter 2 and 3? They are the problems to work on after.

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