

Chapter 1

Introduction

This monograph is devoted to an analysis of a classical mathematical model in population biology, known as the stochastic logistic SIS model. It serves as a model both for the spread of an infection that gives no immunity and for density dependent population growth, and it also appears as an important special case of a contact process that accounts for spatial influences. These three interpretations of the model are further discussed in Chap. 2. In that chapter it is also shown that the SIS model is just one out of a whole family of logistic models. The model is used outside population biology in areas such as the spread of rumours, the spread of technical innovations, and the theory of chemical reactions. The deterministic version of this model takes the form of a nonlinear differential equation that can be solved explicitly, and where a bifurcation phenomenon appears that corresponds to a very powerful qualitative so-called threshold result. We are mainly concerned with the stochastic version of this model, and with establishing counterparts in the stochastic model to the threshold result that holds for the deterministic model.

The deterministic version of the logistic model goes back to Verhulst [74], while the first studies of its stochastic version are due to Feller [26], Bartlett [11], and Weiss and Dishon [76]. The interest in this model grew slowly at first. One sign of this is that the model was not discussed in the influential book on models in mathematical epidemiology by Bailey [7], although references to the papers by Feller and by Weiss and Dishon were included. The model has since then appeared in several contexts. Bartholomew [9] has applied it to study the transmission of rumours, Oppenheim et al. [56] use it as a model for chemical reactions, Cavender [16] uses it as an example of a birth-and-death process, Norden [53] describes it as a stochastic logistic model, while Kryscio and Lefèvre [39], Nåsell [44, 45, 47, 49], and Andersson and Djehiche [4] return to the epidemic context. Kryscio and Lefèvre summarize and extend the work of the previous authors. Cavender [16] and Kryscio and Lefèvre [39] introduce two very useful auxiliary processes discussed below. Nåsell [44] provides extensions of these results. He introduces the important transition region (see below) into the study. Further improvements given in this monograph are based on the papers by Ferrari et al. [27] and by Clancy and Pollett

[18]. Additional work on this and similar models are reported by Grasman [31], Ovaskainen [57], Newman et al. [51], Doering et al. [24], Assaf et al. [6], and Cairns et al. [15].

The stochastic model that we deal with takes the form of a birth–death process with discrete state space and continuous time. Using the language of epidemic modelling, we find that the state of the process gives the number of infected individuals as a function of time in a constant population of N individuals. It takes integer values from zero up to N . The model accounts for two changes in state, corresponding to infection and recovery. The hypotheses of the model specify the rates at which these two changes occur. The model properties can be derived from a linear system of differential equations for its state probabilities, called Kolmogorov equations. The number of variables in this system of equations equals the total number of states, which is $N + 1$.

It is very useful for the analysis to consider the deterministic version of this stochastic model. It can be derived in two different ways. The first way of deriving it, which is common among deterministic modellers, is to interpret the hypothesized transition rates deterministically. This leads immediately to a non-linear differential equation for the number or the proportion of infected individuals. Its solution gives this proportion as a function of time. We see here one important difference between stochastic and deterministic models: The state variable of the latter is not limited to integer values, since it appears in the model as a function of time that is differentiable and therefore continuous.

The second way of deriving the deterministic version of the model is as an approximation of the stochastic one. We are lead to the same differential equation as above after scaling with the population size N and letting N approach infinity. One consequence of this is that the parameter N disappears from the scene in the deterministic setting. The influence of N is important in the stochastic setup, and absent in the deterministic one. The fact that the deterministic model is an approximation of the stochastic one raises the question if the approximation is acceptable. Apparently, acceptability requires the population size N to be sufficiently large. But it is important to agree on what criteria should be used in judging such acceptability. The only way to find out is to do a full analysis of the stochastic model. This is the purpose of the present monograph for the stochastic SIS model. The main mathematical tools that we shall use in this work are taken from the area of asymptotic analysis. We shall develop approximations of the various quantities that are of interest in the stochastic model as N approaches infinity. We strive for approximations that are asymptotic, but we shall not always succeed.

Deterministic modelling has been very successful in many areas of population biology. The important results are qualitative in nature, and are derived from nonlinear deterministic models with bifurcation. These results respond to qualitative questions about the survival or extinction of specific populations. It is not clear what the counterpart to these qualitative results is in the stochastic version of the model, especially since the reason for the qualitative results is nonlinearity in the deterministic formulation, while the nonlinearity is absent in the stochastic formulation. We shall illuminate this question in the simple case of the stochastic logistic SIS model.

It is noteworthy that deterministic and stochastic models disagree qualitatively with regard to the extinction phenomenon. The deterministic version of the SIS model has a threshold. This means that the population of infected individuals is predicted to go extinct if it lies below the threshold, and that it will persist indefinitely if it lies above the threshold. (We note that the threshold is a point in a parameter space. We say that a population lies above (below) the threshold if a certain parameter lies above (below) its threshold value.) In stark contrast to this, we find that the stochastic model predicts that the population of infected individuals will ultimately go extinct as time goes on, regardless of where the population is situated with regard to the deterministic model threshold. However, the time to extinction turns out to be very different above and below the deterministic model threshold; it can be really long above the threshold, in some cases exceeding the age of the universe, while it is short below it. The time to extinction can therefore be used as a kind of counterpart in the stochastic version of the model to the qualitative result represented by the threshold that can be established for the deterministic version of the model. Our study of the time to extinction for the stochastic SIS model will confirm this.

The fact that deterministic and stochastic models disagree qualitatively as just mentioned may appear inconsistent with the property that the deterministic model is an approximation of the stochastic one, but that is not so. As shown in Andersson and Britton [3], the deterministic model solution is an approximation of the solution for the stochastic model only on finite time intervals. Thus, the approximation does not necessarily hold in the limit when time approaches infinity. A consequence of this is that the endemic infection level predicted by a deterministic model corresponds to the quasi-stationary distribution rather than to the stationary distribution in a stochastic model with an absorbing state, as is the case in the model that is studied here.

The threshold phenomenon can be described by a partition of parameter space into regions where model properties differ qualitatively. For the deterministic model it leads to two regions, one above threshold, and the other one below threshold. It is customary to introduce a parameter that is denoted by R_0 and referred to as the basic reproduction ratio, and with the property that the threshold is identified by $R_0 = 1$. The situation is different in the stochastic model. The fact that the extra parameter N is present in the stochastic model has the consequence that this model has three parameter regions where qualitatively different results occur. Two of them correspond roughly to the two regions $R_0 > 1$ and $R_0 < 1$ that are present in the deterministic setup, while the third one is a transition region between the two that appears near the threshold where $R_0 = 1$. The stochastic model parameter region that corresponds to the region where $R_0 > 1$ in the deterministic model can be described in two ways. The first description is purely formal, and based on the fact that we use concepts from the area of asymptotic analysis. The parameter region is then defined by the requirement that $R_0 > 1$ as $N \rightarrow \infty$. However, from a practical standpoint this means that $R_0 - 1$ must be strictly positive for any finite value of N . We shall describe this by saying that R_0 is distinctly above one. The second description of the parameter region where R_0 is distinctly above one is in terms of approximate

boundary values for R_0 that depend on N . These boundary values decrease toward the value one as N increases toward infinity. Similar descriptions apply for the parameter region where R_0 is distinctly below one. The width of the transition region goes toward zero as N becomes large. In the limit as N reaches infinity, the transition region becomes empty, as it is in the deterministic version of the model.

The various manifestations of the stochastic logistic model that we are concerned with all behave in qualitatively different ways in these three parameter regions. Therefore, by necessity we are led to consider separate derivations of our results in each of these regions.

The qualitative difference between deterministic and stochastic models mentioned above has a consequence that is important for our analysis. The counterpart to a stable stationary solution of the deterministic model is not a stationary distribution of the stochastic model, but instead a so-called quasi-stationary distribution. The stationary distribution of the stochastic model is degenerate. It is reached when extinction occurs. However, before extinction it will in many cases be true that the distribution is practically constant. This distribution, called the quasi-stationary distribution, can mathematically be defined as a stationary distribution, conditional on non-extinction. It has a very desirable property from a modelling standpoint. If the system that we are studying has been running for a long time, and if the only thing that we know about it is that it has not reached extinction, then we can conclude that the quasi-stationary distribution is the likely distribution of the state variable. This is one reason for our interest in the quasi-stationary distribution. Another reason is that knowledge about this distribution also gives us information about the remaining time to extinction from this distribution. This is a mathematical result that we make use of in the analysis of the extinction time for the model that we study. Because of these two properties, the quasi-stationary distribution plays a central role in our study of the stochastic SIS model. A bit of history of the concept of quasi-stationarity is given by Pollett [61]. It shows that this concept originated with the two papers by Yaglom [78] and by Bartlett [10]. Even though the Yaglom paper preceded that of Bartlett, it appears that Bartlett's ideas about quasi-stationarity were original and unaffected by Yaglom. Basic theoretical results concerning quasi-stationary distributions for continuous-time Markov Chains with finite state space were later derived by Darroch and Seneta [21]. It is likely that they were inspired by Bartlett, as indicated in Nåsell [50].

It turns out to be impossible to find explicit expressions for the quasi-stationary distribution for any population model with density dependence. Progress therefore rests on finding good approximations. All approximations of the quasi-stationary distribution of the SIS model that we consider in this monograph are based on two auxiliary processes introduced by Cavender [16] and by Kryscio and Lefèvre [39]. These processes are birth–death processes whose transition rates are similar to those of the SIS model itself. An important difference is that the origin has been removed from their state spaces. Thus, they lack absorbing states, and have the same state space as the quasi-stationary distribution. This means that they have non-degenerate stationary distributions that can be determined explicitly. These

stationary distributions, called $\mathbf{p}^{(1)}$ and $\mathbf{p}^{(0)}$, both serve as approximations of the quasi-stationary distribution.

In an early study of the SIS model, Nåsell [44] noted that the components of the quasi-stationary distribution satisfy a certain implicit relation. Moreover, this relation suggested that it should be possible to solve for the quasi-stationary distribution with the aid of iteration, where the stationary distributions $\mathbf{p}^{(1)}$ and $\mathbf{p}^{(0)}$ suggested themselves as natural starting points. Indeed, it turned out that a numerical method based on this iteration scheme seemed to converge. It was therefore natural to imagine that an approximation of the quasi-stationary distribution would be produced by taking just one iteration step. However, it is not clear in what sense an asymptotic approximation after one iteration step approximates the quasi-stationary distribution itself. This weakness with the indicated method can now be resolved.

The iteration method can be described by giving a sequence of iterates, where each one is produced by applying a certain map Ψ to the previous one. This map will be defined in Chap. 3. It was independently defined and studied in the theoretical work by Ferrari et al. [27]. They showed that the sequence of iterates converged to the quasi-stationary distribution for arbitrary initial distributions. A further important property of this map was shown by Clancy and Pollett [18]. They proved that it preserves what is called likelihood ratio ordering. A proof is given in Sect. 3.6. By using this result, we are able to derive asymptotic approximations of the quasi-stationary distribution itself, and not only of the iterates, in the two parameter regions where R_0 is distinctly larger than one and distinctly smaller than one. We shall also provide an approximation of the quasi-stationary distribution in the transition region, but we do not claim that it is asymptotic.

The concept of quasi-stationarity is important for many models in population biology. It is therefore desirable to have access to methods that give information about the quasi-stationary distribution for such models. The methods that are developed in the present study are of value for other models. This is particularly true for univariate logistic models, for which preparations are made in Chap. 3. But it holds also for the two bivariate models where already some work on the quasi-stationary distribution has been reported, namely the Ross malaria model and the classical SIR model with demography, used for studying childhood infections, see Nåsell [42, 46, 50].

There are two aims of the present monograph. One of them is, as mentioned above, to give a useful approximation of the quasi-stationary distribution and of the time to extinction for the stochastic SIS model. The second aim is to describe the methods that we have developed for deriving such approximations in such a way that the reader gains an insight that is useful in work on related stochastic models.

The rest of the monograph is disposed as follows:

Chapter 2 is devoted to model formulation. We give three different population biology situations that lead to similar mathematical models. We show in particular that the SIS model is one out of a whole class of logistic models.

Chapter 3 gives important stochastic process background for our study, to a large part in a more general setting than that provided by the SIS model. We deal with the

quasi-stationary distribution, the time to extinction, and the two auxiliary processes introduced by Cavender [16] and by Kryscio and Lefèvre [39]. We show that the stationary distributions $\mathbf{p}^{(0)}$ and $\mathbf{p}^{(1)}$ of the auxiliary processes are important both for the quasi-stationary distribution and for the time to extinction. Also, we define the map Ψ mentioned above. It is a map between discrete distributions with the property that the quasi-stationary distribution is the unique fixed point of this map. We discuss also concepts and results of stochastic ordering. An important conjecture concerning stochastic ordering for the SIS model pronounced by Kryscio and Lefèvre in 1989 is described. A proof of this conjecture for the SIS model was given by Clancy and Pollett [18]. Because of its importance, it is included here.

We return to the stochastic SIS model in Chap. 4. We give explicit expressions for the stationary distributions $\mathbf{p}^{(1)}$ and $\mathbf{p}^{(0)}$ of the two auxiliary processes introduced by Cavender [16] and by Kryscio and Lefèvre [39]. As mentioned above, these stationary distributions were originally introduced as approximations of the quasi-stationary distribution of the SIS model. In our approach, they are starting points for approximations that lead to the main result that we present, namely a uniform approximation of the quasi-stationary distribution, valid over all three parameter regions. Chapter 4 also contains numerical illustrations that show that the two stationary distributions $\mathbf{p}^{(1)}$ and $\mathbf{p}^{(0)}$ do not provide sufficiently good approximations of the quasi-stationary distribution \mathbf{q} .

Many of the various approximations for the SIS model that are developed in later chapters are based on approximations involving the normal distribution. This type of result is of course completely independent of the particular model that we study. We derive the approximations concerning the normal distribution that we need in Chap. 5. They include asymptotic approximations of sums of normal densities, and of sums of reciprocals of normal densities. Even though the normal distribution has been studied extensively, it appears that these approximation results are new. The results in this chapter are likely to be highly useful in the search for approximations of quasi-stationary distributions of other stochastic models.

Approximations of the stationary distribution $\mathbf{p}^{(1)}$ are derived in Chaps. 6 and 7. The first of these two chapters is devoted to derivations, while the second chapter summarizes the results. Separate approximations are given in each of the three parameter regions. Furthermore, each approximation of the probability $p_n^{(1)}$ is valid only in a restricted interval of n -values. This interval is indicated in each case.

Very similarly, we give approximations of the stationary distribution $\mathbf{p}^{(0)}$ in Chaps. 8 and 9. Again, separate results are given in each of the three parameter regions, and the results hold in restricted n -intervals.

Approximations of images under the map Ψ of the stationary distributions $\mathbf{p}^{(1)}$ and $\mathbf{p}^{(0)}$ are derived in Chap. 10. We give also approximations of the images of $\mathbf{p}^{(1)}$ after multiple applications of the map Ψ . These results are used in Chap. 11 to derive approximations of the quasi-stationary distribution in each of the three parameter regions, again in properly restricted n -intervals.

The expected time to extinction from quasi-stationarity and from the state one can be determined mathematically from the quasi-stationary distribution \mathbf{q} and from the stationary distribution $\mathbf{p}^{(0)}$, respectively. Approximations are given in Chap. 12.

As can be expected, the approximations take different forms in the three parameter regions.

The need to present results separately in three different parameter regions is somewhat unsatisfactory and unelegant. We respond to this by deriving uniform results that are valid over all three parameter regions. Uniform approximations of the two stationary distributions $\mathbf{p}^{(1)}$ and $\mathbf{p}^{(0)}$ and of the quasi-stationary distribution \mathbf{q} are given in Chap. 13. This chapter also contains uniform approximations of the expected times to extinction from the quasi-stationary distribution and from the state one. All these results are new. The uniform approximations are improvements over the results that have been derived separately in each of the three parameter regions.

Chapter 14 discusses thresholds for the stochastic SIS model. Early work on this model used numerical evaluations as a basis for conjecturing the threshold behavior, as described by Nåsell [43]. We show that the approximations that we have derived are consistent with slight variations of these early conjectures.

The monograph finishes with some concluding remarks in Chap. 15.

The monograph is written for a reader who has a good working knowledge about birth–death processes, including methods for their formulation and analysis. There are many text-books that deal with this area of stochastic processes. Two good introductions are the books by Allen [2] and by Taylor and Karlin [71]. Another introduction that can be recommended is the unpublished report by Schmitz [66]. It is particularly appropriate for a reader of the present monograph, since it deals with particularities of the SIS model, including a treatment of its quasi-stationary distribution. It is written in German.

We envision two different readers of this monograph. One of them is mainly interested in what can be said about the quasi-stationary distribution and the time to extinction for the SIS model, while the other one is interested not only in these results, but also wants to understand the methods that we use and to apply them in analysis of quasi-stationary distributions of other stochastic models. The reader in the first category is recommended to go directly to Chaps. 11–15, after reading the introductory chap. 2, and briefly reviewing the contents of Chaps. 3–5. In particular, he is encouraged to skip the rather technical developments that are given in the preparatory Chaps. 6, 8, and 10. The very essence of the results are contained in Sects. 13.4 and 13.5, where we give uniform approximations of both the quasi-stationary distribution and of the expected time to extinction for the SIS model. However, it is important to realize that the results of the intermediate Chaps. 6–10 are all needed in the important development in Chap. 11, where approximations of the quasi-stationary approximation are derived. These intermediate chapters are on the other hand recommended for the reader in the second category. In particular, they will acquaint him with the development of asymptotic approximations, which may be less common knowledge for many persons that work with stochastic models.

There are two appendices to this monograph. The first one gives a summary of the notation that is used, while the second one contains a number of Maple procedures in the form of a Maple module. These procedures can be used to do numerical evaluations of the various quantities that are studied. In particular, they have been used to produce the plots that are included in the monograph.

Extinction and Quasi-Stationarity in the Stochastic
Logistic SIS Model

Nåsell, I.

2011, XI, 199 p. 10 illus. in color., Softcover

ISBN: 978-3-642-20529-3