

Mimmo Iannelli
Andrea Pugliese

An Introduction to Mathematical Population Dynamics

Along the trail
of Volterra and Lotka



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Preface

The preface is that part of a book which is written last, placed first, and read least. As I approach my concluding task I am moved to reflect why a preface should be written at all. This question, if followed into all the intricacies of which it holds potentiality, should apparently result in a composition new in literature, a Preface to the Preface. Such precedent should not be lightly established, for it suggests a vista of future degenerations after the pattern of Josiah Royce's infinite succession of maps, each containing within itself its own replica on a reduced scale. But without going to such lengths as this, the philosophy of the preface may perhaps briefly be summarized to this effect, that it is the author subjective introduction to the more objective matter that should follow. Here he may, if this is deemed of any interest, say something regarding the circumstances that gave origin to the work, and the conditions under which it came into being. He may express his feelings as to its alleged purpose, and may follow custom by giving voice to pious wishes as to the function which the product of his presumptive mind may fulfill in an Universe in which no event, however trivial -be it no more than the addition of one more book to the groaning library shelves- is without distant reverberations.

A.J. Lotka "Elements of Mathematical Biology", 1924

Almost a century has passed since Alfred Lotka wrote the preface to his book, whose title alone reveals the intention to be founding of Mathematical Biology as a new branch of Applied Mathematics. And indeed, in his view Mathematical Population Dynamics had a major role within the discipline to come.

After such a long lapse of time and such various and widespread developments concerning the interplay of Mathematics and Biology, we actually need to start our introduction considering what Mathematical Biology is today. In fact, the recent decades have seen an explosion in the use of mathematical methods in all areas of biology, from the use of advanced statistical methods in the analysis of medical trials, or in the alignment of DNA segments, to sophisticated pattern recognition methods in the analysis the signals from electroencephalogram data or the inference of vegetation structure from remote-sensing data.

This explosion may correspond to the joint high developments of specific mathematical methodologies and powerful implementation on computers, that contribute to make the Universe evoked by Lotka, full of reverberations difficult to follow and to understand in a unified view. Thus our work necessarily covers only part of this Universe, both concerning the object of our interest among the many fields of Biology, and our approach and methods of analysis within Mathematics, in short our idea of Mathematical Biology.

Actually, our view of Mathematical Biology, more or less corresponds to the scope of the journals or societies that have “Mathematical Biology” in their names as a distinctive character.

By “Mathematical Biology” we intend the use of mathematical models aiming at describing quantitatively and understanding the processes behind the data that have been observed and collected. In our view, mathematical biologists should not be satisfied in finding that, for instance, a parabola fits some data and can be used to make predictions; they should strive to understand the mechanisms yielding the parabola as a consequence of the laws they obey to. Indeed, mathematical modeling, in this sense, is becoming topical in all areas of biology, as can be seen from the very large number of publications involving mathematical modeling that can be found in generalist or specialized scientific journals. And still it would be impossible, not the least because of our limited knowledge, writing even an introduction to such a diverse field, and we were forced to make choices.

Biological systems are extremely complex and idiosyncratic. The case of Population Dynamics is emblematic, since a mathematical model that fits very well some data relative to a given species, may miss some factors that are quantitatively important in another one. Generally a model aiming at an accurate and quantitative fit to data must involve hundreds of relevant variables, and its properties may be understood only from numerical simulations at a computer. We see nothing wrong with that kind of models, but our basic choice here is to emphasize simple models that generically (i.e. over a reasonable range of parameter values) yield patterns in qualitative agreement with characteristic features of the biological phenomenon under study. In fact, in our view, understanding what are the consequences of model structure and assumptions in simple cases is essential also when one attempts to build a complex model, and to understand the result of its simulations.

Our work is focused on the mathematical theory of Population Dynamics, an area where mathematical biology has generated new concepts that can be understood in their own. Initially, we thought we could include in this book other topics in Mathematical Biology such as molecular networks (how biomolecules can interact, and what are the consequences at the system level) and excitable media (a theory explaining phenomena such as neural impulse or cardiac beat); we believe that models in these areas share methods and approach with the models in population dynamics considered here, and a reader could find insightful connections between different topics. However, the need to limit the time needed to complete the book, and its number of pages forced us to conclude our work without going beyond ecological models.

What is there in this book, then? We follow a tradition that goes back to Lotka and Volterra, and use it as the area where to understand different types of mathematical modeling, and the possible meaning of qualitative agreement of modeling with data. Thus, Ecology is the basic scenario including also a part devoted to the spread of infectious diseases, an area where mathematical modeling is extremely popular, and is at the center of our current research. Our ambition was to follow the trail opened by Volterra and Lotka, to show where and how a century of modeling effort has conducted both Mathematics and Biology.

The material in this book has been used, in draft or oral form, in the courses (formerly *Biomatematica*, recently *Mathematical Biology*) we have been teaching at the University of Trento for more than 20 years. The courses have been aimed at students at their fourth year of studies in Mathematics, and this can presumably be seen in the structure of the book. We consider this book mainly as an introduction to *Mathematical Biology* for students with no experience in *Biology*, but with some mathematical background; in particular, we expect that readers have a reasonable working knowledge of calculus, mathematical analysis, linear algebra, probability theory and differential equations, although in the appendices we present the specific results we use in this book. We should also mention that, though we have not explicitly introduced and discussed the use of numerical methods for producing simulations, we strongly encourage the students to use their computer abilities and the available software to explore the models, check the theoretical findings, guess the behaviors beyond the analytical results.

The chapters aim at giving an idea of the biological problems that are examined, at presenting clearly the biological assumptions and the mathematical elaborations on those, and at discussing the biological insights, if any, that have been reached through the mathematical modeling. At the end of each chapter we propose a set of problems that ask the student to make an effort to go beyond the matter presented in the text. Thus most of them are not quite routine exercises, but they ask to try to proceed further in the modeling task and in the use of mathematical tools. For this reason some of the problems may not have a unique answer, but serve as a stimulus for discussion.

In the text some mathematical steps are proved in detail, while for others we ask the readers a leap of faith or the consultation of more advanced material; in all cases, however, we attempt to keep a clear distinction between what is a biological assumption, what a mathematical theorem (though we rarely use that term), what an approximation and what a reasonable conjecture, sometimes based on extensive numerical simulations. In this sense, we consider this book mainly a book of mathematics, that aims to give an idea of how mathematics is used in biological applications, without necessarily showing the most advanced results obtained, or the most advanced models examined.

We hope that the book can be of interest for everybody (student, researcher or other) looking for a first introduction to how to use mathematical modeling in biology. These are our pious wishes as to the function of our product in the Universe of Lotka who, as you see, indeed wrote a “Preface” to the Preface.

Trento
March 2014

Mimmo Iannelli
Andrea Pugliese

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Since this book took its shape through many years, it is difficult to trace back all the suggestions we directly received by colleagues and students, to convey our special thanks to all of them and, indeed, their list would be very long. We would only mention those who helped us during the conclusive part of our writing: Odo Diekmann and Gianpaolo Scalia-Tomba, for their useful remarks on some parts of the manuscript, Marco Sabatini for his competent advice on a result we used, and Lorenzo Bramanti for providing us his personal pictures of corals, one of which is on the cover of this book.

On the other hand, we may say that our work has been influenced by the many inputs from the scientific world and by the many actors of the scientific adventure that, gathering the heredity of Lotka and Volterra, built Mathematical Biology through the last forty years, so our thanks go to them for their being our inspiring examples. Beyond the many books and articles that have inspired one chapter or another (and they are duly cited), we are particularly indebted to the book by Renato Casagrandi, Giulio De Leo and Marino Gatto, ‘101 problemi in ecologia’, McGraw-Hill, a remarkable collection of problems connecting models with ecological problems and data.

We also thank Springer-Italia for giving us the opportunity of transforming our draft notes into a real book and in particular the Editors Francesca Bonadei and Francesca Ferrari, for their help and patience during our delayed writing.

Moreover, we have to thank our students through the years, for having answered to the call and having given us credit, when we started to teach something unusual for a curriculum in Mathematics, sometimes very demanding for the wide range of mathematical theories and methods necessary to analyze the models.

And, also, this book is dedicated to the future students who will accept to be challenged providing a precious feedback to our teaching and will contribute to improve and develop the contents of the present version.

The Authors

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Part I
The growth of a single population

Malthus, Verhulst and all that

Apparently, no book has been so extensively discussed by people who seem not to have read it, as it happens with the “Essay on the Principle of Population” by Mr. Malthus.¹

Such a harsh note by the editor, against the comments received by the *Essay* [9], takes us back to the atmosphere of those times and to the discussions that the *Principle of population* sustained by Thomas Robert Malthus, caused and fed since the first edition of the book in 1798. Actually this Principle can be stated in a few words:

population, when unchecked, increases in a geometrical ratio; subsistence increases only in an arithmetical ratio.

Projected to the future, such a mechanism produces catastrophic scenarios that, rightly or wrongly, when the *Essay* was published, were the object of great discussions and quarrels (see [10] and the introduction to that volume, in Italian, for an interesting presentation). In fact, the thesis presented by Malthus in his famous book is part of a wide discussion between the conservative views (supported by Malthus) and the optimistic ones of the Enlightenment philosophers (especially Godwin and Condorcet) who supported a *Theory of Progress*. Right or wrong in his conclusions, Malthus however deserves the merit of having pointed out, about two hundred years ago, the problems related to demographic expansion.

Since the publication of the *Essay*, the name of Malthus is associated to *exponential growth* and in fact the model we will present at the beginning of this chapter is named after him. Actually, in the context of the *Essay*, as in other demographic studies, the use of an exponential curve to fit experimental data is essentially empirical, while the modeling viewpoint that we introduce in Sect. 1.2 aims at obtaining exponential growth as the consequence of *a priori* constitutive assumptions. This approach will be maintained throughout the chapter where different mechanisms regulating intraspecific competition and exogenous effect will be introduced and discussed.

¹ A note by the editor to “Summary View on the Principle of Population” by T.R. Malthus, 1830.

1.1 A look at exemplary data

The empirical approach to data description can be conveniently illustrated by exemplary data from the demographic context. In fact in Table 1.1 we present classical numbers of a human population, provided by census institutions. Actually, demographic data have received much attention for thousands of years since, as it is obvious, man has initially paid much attention to most important events like births, deaths, diseases ... Thus we can take advantage of rather accurate observations.

In Table 1.1 data are reported by 10-years steps and the third column shows the *growth rate* of the population, i.e. the yearly relative change of the population. Namely, if N_i denotes the number of individuals in the year i and h the length of the time interval (in the table $h = 10\text{ years}$), then the growth rate can be defined through the formula

$$\alpha = \text{growth rate} = \frac{N_{i+1} - N_i}{h N_i}.$$

When the growth rate is approximately constant (as in the first part of Table 1.1, but also for the years 1900–1930) data can be represented through an exponential curve. In fact, we have the equation

$$N_{i+1} = (1 + \alpha h)N_i \tag{1.1}$$

Table 1.1 U.S.A. population

<i>year</i>	<i>individuals</i> ^a	<i>rate</i> α
1790	3,929	
1800	5,308	0,035
1810	7,240	0,036
1820	9,638	0,033
1830	12,861	0,033
1840	17,064	0,033
1850	23,192	0,036
1860	31,443	0,036
1870	38,558	0,023
1880	50,189	0,030
1890	62,980	0,025
1900	76,212	0,021
1910	92,228	0,021
1920	106,021	0,015
1930	123,203	0,016
1940	132,165	0,007
1950	151,326	0,015
1960	179,323	0,019
1970	203,302	0,013
1980	226,456	0,011
1990	255,712	0,010
2000	285,003	0,013

^a millions

and, iterating from $i = 0$ we get

$$N_i = (1 + \alpha h)^i N_0,$$

and we see that the population undergoes geometrical increase or decrease if $\alpha > 0$ or $\alpha < 0$ respectively.

If now we suppose that (1.1) holds for h small enough, the previous formula can be written using the exponential function as

$$N_i = N_0 e^{rhi}, \quad \text{with} \quad r = \frac{\ln(1 + \alpha h)}{h},$$

and, adopting a time-continuous framework, for a given fixed time t the number of individuals $N(t)$ is approximately given by

$$N(t) = N\left[\frac{t}{h}\right] = e^{rh\left[\frac{t}{h}\right]} N_0 \cong e^{rt} N_0 \quad (1.2)$$

where we have approximated

$$h \left[\frac{t}{h} \right] \cong t,$$

and the approximation is better as h is smaller.

A procedure to fit data with an exponential curve, estimating the “best” value of the parameter r , is to apply the *least square method*, fitting a line to the data of Table 1.1, represented in logarithmic scale. Namely, in such a scale, the exponential (1.2) is transformed into the line

$$y(t) = \ln N(t) = rt + \ln N_0$$

with slope r and intercept $y_0 = \ln N_0$. Then, the least square procedure applied to the data of Table 1.1 provides the following values

$$r = 0.02, \quad P = 0.96,$$

where P is the Pearson coefficient; the result of the fit, not quite satisfactory, is shown in Fig. 1.1. However if we restrict to data up to the year 1860, we get

$$r = 0.029, \quad P = 0.999$$

and the agreement is much better (Fig. 1.2a). The same procedure applied to data in the time interval 1910–2000, gives also a satisfactory result (Fig. 1.2b)

$$r = 0.0126, \quad P = 0.997.$$

We have thus seen that, within certain limits, exponential growth provides an empirical description of data. In the next section we set up a different (modeling)

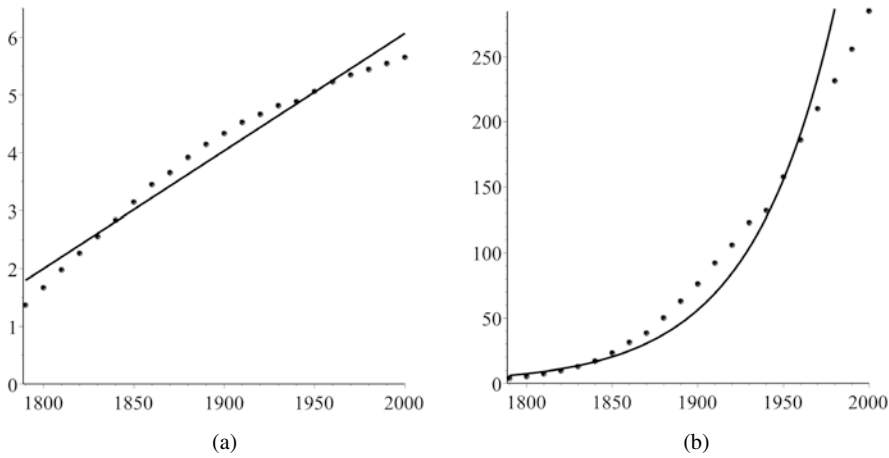


Fig. 1.1 Exponential fit of U.S.A. population in the years 1790–2000: (a) logarithmic scale; (b) the exponential curve

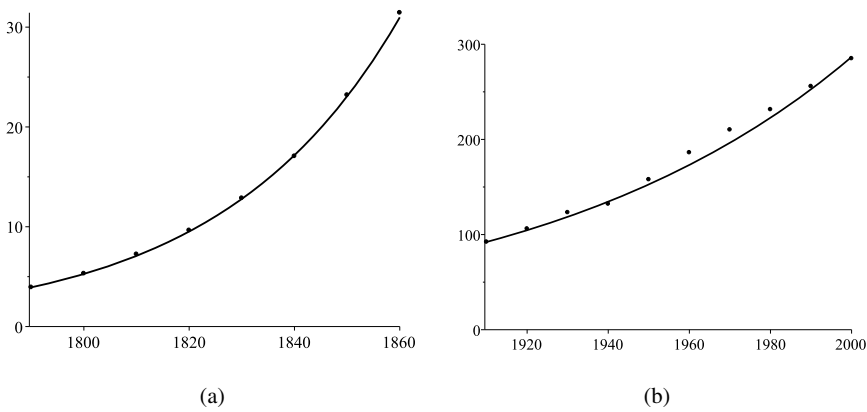


Fig. 1.2 Exponential fit of U.S.A. population: (a) years 1790–1860; (b) years 1910–2000

viewpoint to get again exponential growth as a consequence of constitutive a priori assumptions. Specifying these assumptions will allow us to define the limits within which we expect the model to work and the modifications that may be necessary beyond these limits.

1.2 Malthus model

The mathematical model named from T.R. Malthus is the simplest model to describe the growth of a single population and is based on a few assumptions that apply to an idealized situation. Namely we assume that:

- the population is *homogeneous* (all individuals are identical);
- the population is *isolated* (there is no immigration nor emigration);
- the habitat is *invariant* (the amount of resources and the life conditions are not influenced by external factors nor by the population itself);
- the population is *very large* (stochastic events and fluctuations can be neglected).

Actually, these assumptions about environmental conditions can be sometimes realized in laboratories for some species of simple organisms, at least for a period of time sufficiently short. Though these conditions can rarely be satisfied in field situations, the corresponding model, albeit very simple, is able to provide a good description of data in some specific cases.

Under the above assumptions, since all individuals are identical, their number $N(t)$ is the only variable necessary to describe the state of the population as a function of time. Moreover, because the population is large, we can adopt a continuous framework for the number of individuals. Thus, though $N(t)$ is intrinsically a discrete function, we will take it as a real function of the real variable t .

Concerning the birth and death processes, they are the unique ways for $N(t)$ to change. In fact, the population is isolated and, since the habitat is invariant, fertility and mortality do not change with time nor depend on $N(t)$. Namely, the two processes can be regulated by the following assumptions:

- within a (short) time period of length Δt , each individual gives, on average, birth to $\beta\Delta t$ new individuals;
- within the same time period Δt , each individual has probability $\mu\Delta t$ of dying;

where the parameters $\beta \geq 0$ and $\mu \geq 0$, are respectively called *fertility* and *mortality*.

By the previous assumptions we have

$$\frac{N(t + \Delta t) - N(t)}{\Delta t} = (\beta - \mu)N(t)$$

and, going to the limit as $\Delta t \rightarrow 0$, we get the following equation

$$N'(t) = \beta N(t) - \mu N(t) = (\beta - \mu)N(t), \quad (1.3)$$

that represents *Malthus model*. The parameter

$$r = (\beta - \mu)$$

is the (instantaneous) *growth rate* and is also called *Malthus parameter* or *biological potential* of the population.

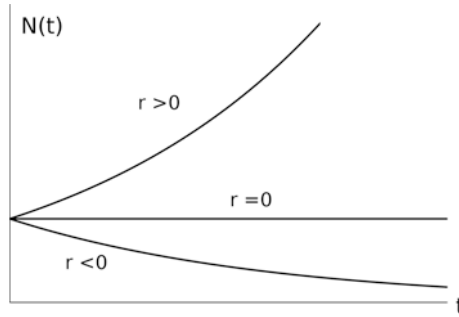


Fig. 1.3 Solutions to the Malthus model

With the initial condition

$$N(0) = N_0$$

the evolution of the population is completely determined. In fact, the solution to (1.3) is

$$N(t) = N_0 e^{rt}$$

and we see that the population will go to extinction or will grow without limits if $r < 0$ or $r > 0$, respectively. If instead $r = 0$, the population size is constant (births and deaths compensate, see Fig. 1.3). Thus, the *Population principle* stated by Malthus descends from the assumptions of this model.

Mean life of the population

If we disregard the input of new individuals due to births, μ determines the (exponential) decay of a given initial group of individuals

$$N(t) = N_0 e^{-\mu t}. \quad (1.4)$$

If the initial group is composed of newborns (in this case the group is said to be a cohort), then time t corresponds to age of the individuals of the group and, using the symbol a instead of t , the function

$$\Pi(a) = e^{-\mu a} \quad (1.5)$$

may be interpreted as the survival probability, i.e. the probability to survive up to age a . Hence, the function

$$L(a) = \mu e^{-\mu a}$$

can be viewed as the probability density of life duration. Thus the mean life of

the population is given by

$$\tau = \int_0^\infty aL(a)da = \frac{1}{\mu}.$$

One can obtain this result through an integration by parts, or through

$$\tau = \int_0^\infty \Pi(a)da.$$

In fact, for a general random variable $X \geq 0$, its expected value is given by

$$\mathbb{E}[X] = \int_0^\infty \mathbb{P}[X > a]da.$$

In our case X is the age of death and $\mathbb{P}[X > a] = \Pi(a)$.

Note that in the previous discussion age comes into only as an interpretation of time, but it is not a variable of the model. Models including age as a variable will be presented in Chap. 2.

Malthus model applies in the demographic context as well as in other situations. Exponential growth is actually typical of all those situations in which the population can be considered as homogeneous and life conditions do not vary. In particular the model apply to cells, bacteria or to complex living organisms, when the population *invades* or *colonizes* a new habitat. We may discuss further the role and the interpretation of the two parameters β and μ that determine the behavior of the population. In particular, in one of the commentary boxes, the relationship between mortality and the *duration of life* is illustrated. A second box is devoted to the introduction of the *basic reproduction number*, a dimensionless parameter related to reproduction.

The basic reproduction number

We consider the non-dimensional parameter

$$R_0 = \beta\tau = \frac{\beta}{\mu} \quad (1.6)$$

called *basic reproduction number*. R_0 is the average number of newborns produced by one individual during his whole life.

Then, if we take τ as the time unit, transforming time t into $\tilde{t} = \frac{t}{\tau}$ we have to consider the new function $\tilde{N}(\tilde{t}) = N(\tau\tilde{t})$ and eq. (1.3) becomes

$$\frac{d}{d\tilde{t}}\tilde{N}(\tilde{t}) = \tau N'(\tau\tilde{t}) = (R_0 - 1)\tilde{N}(\tilde{t}) \quad (1.7)$$

showing that

- i) if $R_0 > 1$ the population increases,
- ii) if $R_0 < 1$ the population goes to extinction.

Namely, the condition

$$R_0 > 1 \tag{1.8}$$

is a condition for invading the habitat since, under this condition, the population is able to settle and grow, even starting with a small group of individuals. We recall that eq. (1.7) is valid only if $N(t)$ is large enough, so that one may think that the previous comment about small populations is inappropriate. Indeed, an adequate treatment of the settlement phase would require a stochastic model that will be introduced and discussed in Chap. 4, however we will see that the basic reproduction number plays a similar role in the stochastic context.

The interest of introducing this parameter R_0 is in that it is dimensionless and then does not depend on the time unit. It is intrinsic to the model and able to predict the ultimate behavior of the population. This is also an example of how one can rescale the equation of a model in order to point out significant combinations of parameters and also to reduce their number. We will often perform such scaling in other models that will be treated in the rest of the book.

The previous discussion, and the comparison with observational data carried out in the previous section, shows that the assumptions of Malthus model, though capturing some basic aspect of population growth, are somewhat too simple. Populations may grow exponentially only for limited periods of time, as can be seen also from the data on U.S.A. population. We understand that the model must be modified in its basic assumption to include effects that make an exponential curve inadequate to represent data. Next sections are devoted to extensions of the model obtained relaxing those assumptions and introducing significant mechanisms of population growth.

1.3 First extensions of Malthus model: exogenous variability

As we already observed, the basic assumptions stated at the beginning of the previous section simplify too much the description of real phenomena and limit very much the use of the model. The first of them, the assumption of *homogeneity* is however a basic assumption characterizing many models we will be concerned with. In particular, when we will discuss interaction among species, we will consider each species as homogeneous. This *structuring* level corresponds to much observational work on the field and in laboratory investigation. Deterministic models based on the homogeneity assumption consist of ordinary differential equations, while models accounting for spatial spread and/or age structure consist of partial differential

equations and are mathematically more complex. In Chap. 2 and Chap. 5 we will present some of these models.

As far as the other assumptions characterizing Malthus model are concerned, we can first introduce a couple of simple extension that provide a more realistic model.

The first modification concerns *immigration*, in fact a simple change in Malthus model allows to take into account the effect of a constant *migratory flux*. We consider the following equation

$$N'(t) = rN(t) + m \quad (1.9)$$

where we have introduced the *immigration rate* m , defined as

$m = \text{number of individuals entering the population in the time unit.}$

The explicit solution of (1.9), corresponding to an initial datum N_0 , is

$$N(t) = \left(N_0 + \frac{m}{r}\right) e^{rt} - \frac{m}{r},$$

and we see (Fig. 1.4) that, if $r < 0$ ($R_0 < 1$), the immigration sustains the population at an asymptotic size

$$\lim_{t \rightarrow +\infty} N(t) = -\frac{m}{r} = \frac{m\tau}{1 - R_0}.$$

Next we consider the third assumption of the Malthus model and discuss habitat variability. We note that two class of factors contribute to modify life conditions of a population. On the one hand there are factors (such as temperature or other climatic variables) producing *exogenous variability*, that is independent of the population itself; on the other hand, there are *endogenous mechanisms*, i.e. depending on population size, accounting for the many pathways through which the population modify its own life conditions. We start considering the first case, modifying Malthus model by assuming that the rates are explicitly time dependent. Thus we are led to consider

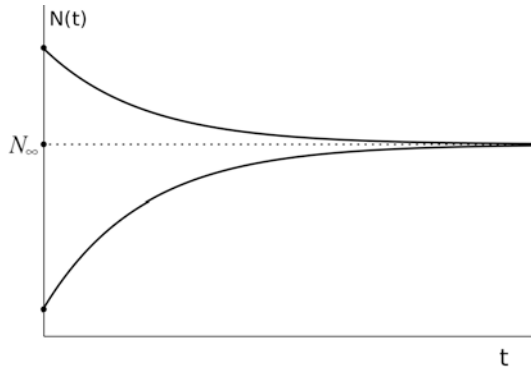


Fig. 1.4 Malthus model with immigration in the case of a negative growth rate. Here $N_\infty = -\frac{m}{r}$

the problem

$$N'(t) = r(t)N(t), \quad N(0) = N_0 \quad (1.10)$$

where the explicit time dependency of the Malthus parameter $r(t)$ describes the trend of the habitat variability. The solution of (1.10) is

$$N(t) = e^{\int_0^t r(\sigma) d\sigma} N_0$$

and its asymptotic behavior depends on the limit

$$r^* = \lim_{t \rightarrow +\infty} \frac{1}{t} \int_0^t r(\sigma) d\sigma.$$

In fact, if the limit above exists and $r^* \neq 0$, then, for any $0 < \varepsilon < |r^*|$, for t sufficiently large we have

$$r^* - \varepsilon \leq \frac{1}{t} \int_0^t r(\sigma) d\sigma \leq r^* + \varepsilon$$

and consequently

$$N_0 e^{(r^* - \varepsilon)t} \leq N(t) \leq N_0 e^{(r^* + \varepsilon)t} \quad (1.11)$$

showing that the growth or extinction of the population is approximatively exponential with rate r^* .

In the case of a time periodic Malthus parameter

$$r(t+T) = r(t),$$

describing for instance seasonal variations, climate cycles or epochal trends, r^* is the mean over one period of the Malthus coefficient (see Problem 1.2)

$$r^* = \bar{r} = \frac{1}{T} \int_0^T r(s) ds. \quad (1.12)$$

Moreover, in this case, one has a result more precise than (1.11), since we have

$$N(t) = e^{\bar{r}t} N_\pi(t), \quad (1.13)$$

where $N_\pi(t)$ is a periodic function. Thus the growth is an exponential tuned by oscillations (see Fig. 1.5).

1.4 Endogenous variability of the habitat

Concerning *endogenous* variability of the habitat we have to modify Malthus model to include all possible factors that influence species growth, through the many possible effects that the presence of the population produces on the habitat. In particular we will assume that both fertility and mortality (*vital rates*) depend on population size N , according to assumptions that describe the specific effects of the population

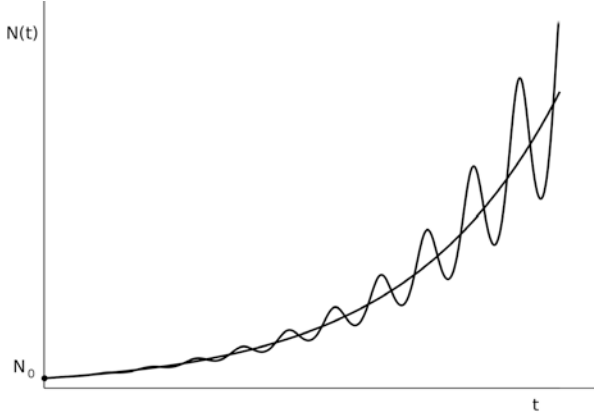


Fig. 1.5 Malthus model with a periodic rate and positive mean \bar{r} , compared with $N_0 e^{\bar{r}t}$

itself on the rates. The growth rate

$$r(N) = \beta(N) - \mu(N) \quad (1.14)$$

will depend on N through specific constitutive forms that translate into a model the interaction mechanisms that need to be included. Thus, a sufficiently general model for the growth of a single species consists in a single ODE equation of the form

$$N'(t) = r(N(t))N(t) = F(N(t)) . \quad (1.15)$$

Since $N(t)$ represents a non-negative variable, we expect that for a non-negative initial datum $N(0)$ the solution of (1.15) is also non-negative. Indeed, since any solution satisfies

$$N(t) = N(0)e^{\int_0^t r(N(s)) ds}, \quad (1.16)$$

we see that this condition is satisfied.

A first step in the analysis of the model concerns existence of equilibria, i.e. constant solutions corresponding to the roots of the function $F(\cdot)$. For a model such as (1.15) we always have the *extinction equilibrium* $N_0^* = 0$ while other possible non-trivial equilibria correspond to the zeros of the growth rate

$$r(N_i^*) = 0.$$

Since

$$F'(0) = r(0)$$

the stability of the extinction equilibrium is related to the sign of $r(0)$. Actually, $r(0)$ plays the role of *intrinsic Malthusian parameter*, i.e. the growth rate at a very low population size such that no influence on the habitat is exerted. Thus, if N_0 is

sufficiently small we have $N(t) \approx 0$ in a first sufficiently short time interval, and

$$N'(t) \approx F'(0)N(t)$$

so that the solution of (1.15) is approximated by an exponential

$$N(t) \approx N_0 e^{r(0)t} \quad (1.17)$$

and, at its initial stage, the population undergoes Malthusian growth. If $r(N)$ is expressed as in (1.14), then we have the condition for invasion

$$R_0 = \frac{\beta(0)}{\mu(0)} > 1$$

expressed through the basic reproduction number (see (1.8) in Sect. 1.2). Invadability is a local concept, meaning that the population can colonize the habitat when the initial size of the population is small.

Different scenarios are possible, depending on the nature of the non-trivial equilibria, i.e. on the nature of the mechanisms regulating the species growth. Through the following sections we will examine some special significant cases.

Model well-posedness

The concept of well-posedness of a mathematical problem was introduced by Hadamard in connection with partial differential equations (see for instance [4]). The idea behind the concept is that a mathematical description of deterministic phenomena must satisfy some basic conditions corresponding to natural properties of the phenomena itself. Hadamard developed his viewpoint within the context of physical phenomena and of Cauchy problems, stating that the problem should be endowed of existence and uniqueness of a solution together with continuous dependence on data (see Appendix A). The concept was resumed by Hille and Phillips [5] in connection with the abstract Cauchy problem and the theory of semigroups.

In our framework, to have a model suitable for a significant description of the real world, we require that the solution not only exists and is unique, but is also non-negative and global in time.

In the case of Equation (1.15) positiveness of the solution follows from (1.16), moreover we assume that

$r(N)$ is continuously differentiable and bounded from above,

because, in fact, this condition guarantees existence, uniqueness, continuity on initial data and boundedness of the solutions on finite intervals.

1.5 Intraspecific competition: the logistic effect

One of the basic principles related to the negative effect of crowding claims the existence of the so called *logistic effect*, that can be stated in words as follows:

an increase of the population size produces a fertility decrease and a mortality increase; since resources are limited, if the population size exceeds some threshold level, the habitat cannot support the growth.

This simple statement tries to summarize the complex phenomenology of *intra-specific competition* due to many factors such as resource availability, habitat pollution and waste, predation increase, energy consumption for social organization. Namely the principle tries to represent the effect of all possible mechanisms that slow down species growth through many possible pathways (see for instance [11]).

A mathematical formulation of the principle corresponds to the following constitutive assumption on $r(N)$:

$$r'(N) < 0, \quad \lim_{N \rightarrow +\infty} r(N) < 0. \quad (1.18)$$

Note that if the intrinsic Malthusian parameter $r(0)$ is negative, then the extinction equilibrium is the only possible equilibrium and the population goes to extinction. If instead $r(0) > 0$ then there exists a unique non trivial equilibrium $N^* = K$ (see Fig. 1.6) which is globally asymptotically stable, because

$$F'(N^*) = r'(N^*)N^* < 0.$$

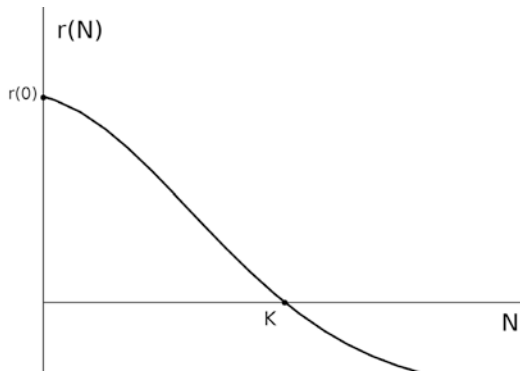


Fig. 1.6 A possible form of the growth rate modeling the logistic effect

Then, in the latter case the solution has the following asymptotic behavior:

- if $0 < N_0 < K$ then $N'(t) > 0$ and $\lim_{t \rightarrow +\infty} N(t) = K$;
- if $N_0 > K$ then $N'(t) < 0$ and $\lim_{t \rightarrow +\infty} N(t) = K$.

The parameter K is usually called *carrying capacity* and, according to this model, whatever is the initial datum $N_0 > 0$, the population attains the carrying capacity K , instead of growing without limits. An example is shown in Fig. 1.7, where the solutions shows the typical behavior of such a model.

The simplest way to include the logistic effect into a model, i.e. satisfying (1.18), is to suppose that fertility decreases and mortality increases linearly with the number of individuals; namely

$$\begin{aligned}\beta(N) &= \beta - \tilde{\beta}N \\ \mu(N) &= \mu + \tilde{\mu}N\end{aligned}$$

where $\beta, \tilde{\beta}, \mu, \tilde{\mu}$, are non-negative constants. With these changes, the growth rate has the form

$$r(N) = \beta(N) - \mu(N) = r - \alpha N \quad (1.19)$$

where $r = \beta - \mu$ and $\alpha = \tilde{\beta} + \tilde{\mu} > 0$. Note that either $\tilde{\beta}$ or $\tilde{\mu}$ can be null, but not both, otherwise there is no logistic effect.

When $r > 0$, using the definition of the carrying capacity K , we find $K = r/\alpha$, then the model is usually written as

$$\begin{cases} N'(t) = r \left(1 - \frac{N(t)}{K} \right) N(t) \\ N(0) = N_0 \end{cases} \quad (1.20)$$

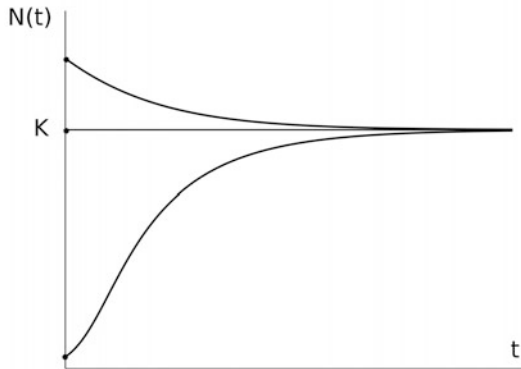


Fig. 1.7 Generic behavior of the solutions of eq. (1.15) under the logistic effect

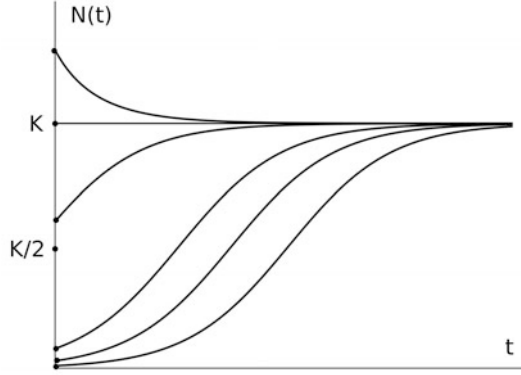


Fig. 1.8 Solutions of Verhulst equation (1.20)

Note also that, if $\tilde{\beta} > 0$, $\beta(N)$ becomes negative for $N > \beta/\tilde{\beta}$, so that the model seems not to be reasonable. However, with realistic values of the parameters, this may occur only for N much larger than K , beyond the sizes one can expect to observe.

Model (1.20) is actually the prototype of all models based on the logistic principle and is called *Verhulst model*, from the name of P. Verhulst who, some decades after Malthus, participated in the discussion about population explosion, proposing this model with in mind the human population (see [12]) and naming it *logistic equation*.

Problem (1.20) can be easily solved explicitly as a Bernoulli equation obtaining

$$N(t) = K \frac{N_0}{N_0 + (K - N_0)e^{-rt}}. \quad (1.21)$$

The graph of $N(t)$, for different values of N_0 , is shown in Fig. 1.8. If $N_0 < K/2$ we have the so called *logistic curve* or *sigmoid* that can be adopted to fit data observed in experimental cultures of bacteria and other micro-organisms. Some classic examples of these cultures are shown in Fig. 1.9. These are experimental curves by G.F. Gause (see [3]) relative to *Paramecium aurelia* and *Glaucoma scintillans*.

We note that, in this model, the parameter r is supposed to be positive (this means $R_0 > 1$), consequently assuming that the population is able to invade the habitat. The meaning of the model stays in that the logistic mechanism stops the exponential growth (1.17) when the population reaches a certain size.

It is interesting to note that model (1.20) can be rescaled to obtain a non-dimensional equation. In fact, taking as a new unit time $\tau = \frac{1}{r}$, and performing the transformation

$$t \rightarrow \tilde{t} = \frac{t}{\tau} = rt, \quad N \rightarrow u = \frac{N}{K}$$

we get the new equation

$$u'(t) = (1 - u(t))u(t). \quad (1.22)$$

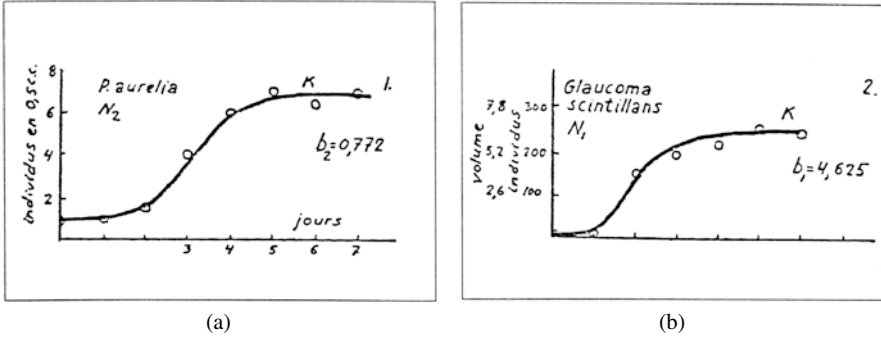


Fig. 1.9 Gause experimental curves: (a) *Parametium aurelia*; (b) *Glaucoma scintillans*. From [3]

where we use again t instead of \tilde{t} for notation simplicity. This shows that there is essentially only one logistic equation and that solutions to model (1.20) for different values of the parameters can be obtained re-introducing parameters into the unique form of the solution of (1.22)

$$N(t) = K u(rt).$$

Though Verhulst model is widely used, other specific form of the growth rate have been proposed to model the logistic effect through assumption (1.18). This may be done either to better fit data or to stress different ways of reacting to population pressure. The special class

$$r(N) = r \left(1 - \left(\frac{N}{K} \right)^\theta \right), \quad \theta > 0$$

shown in Fig. 1.10a, is called θ -logistic form. The corresponding solution curves are drawn in Fig. 1.10b for different values of θ .

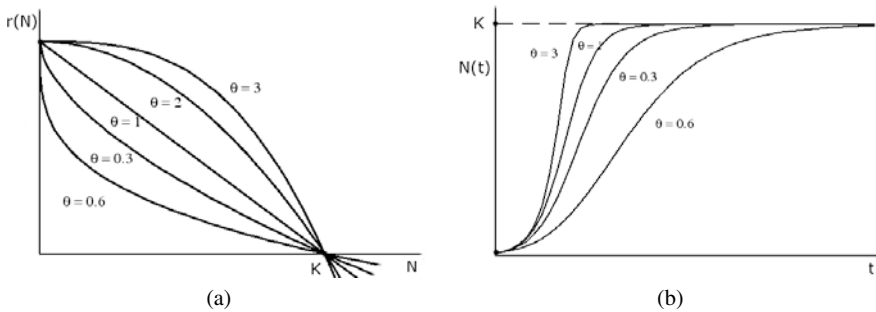


Fig. 1.10 The θ -logistic model: (a) the growth rate for different values of θ ; (b) comparison of solution curves for different values of θ

1.6 The Allee effect

While the logistic effect, generally occurring at high population size, is related to the negative effect of crowding, another effect called *Allee effect* is instead based on another principle stating that:

at low population density, an increase of population size may produce better conditions for life.

This principle actually apply to those species whose survival depends on cooperation so that, when the population size is small, life conditions become worse. This mechanism (see [1]) is relevant at low values of the number of individuals N : the need of cooperation may be so strong that the growth rate may be negative if the population size is below a certain threshold. In order to define a global model, we have to take into account also the logistic effect previously discussed, so that we end up in the following constitutive assumption for the growth rate $r(N)$:

there exists N_m such that

$$\begin{aligned} i) \quad & r'(N) > 0 \quad \text{for } N < N_m, \quad r'(N) < 0 \quad \text{for } N > N_m, \\ ii) \quad & r(N_m) > 0, \quad \lim_{N \rightarrow \infty} r(N) < 0. \end{aligned} \tag{1.23}$$

Condition (1.23) implies that there exists at least an asymptotically stable equilibrium at $N = K > N_m$ and possible forms of $r(N)$ are shown in Fig. 1.11. Figure 1.11a shows the case $r(0) > 0$ (*weak* Allee effect) where only the equilibrium $N = K$ exists and the conclusions we draw are qualitatively the same as for the Verhulst model; the case $r(0) < 0$ (*strong* Allee effect), shown in Fig. 1.11b, is quite different because it

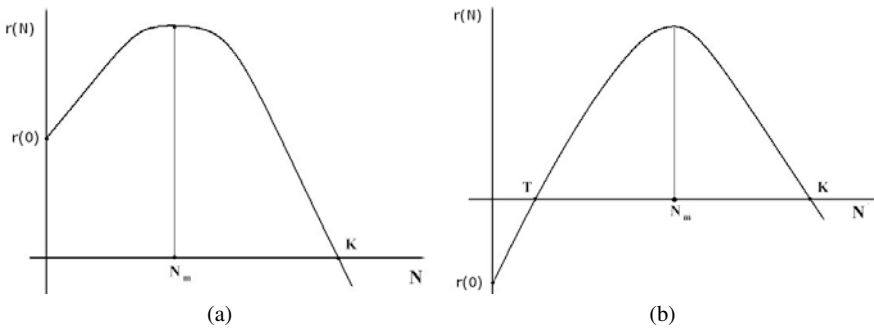


Fig. 1.11 The growth rate in the case of an Allee effect: (a) *weak* Allee effect; (b) *strong* Allee effect

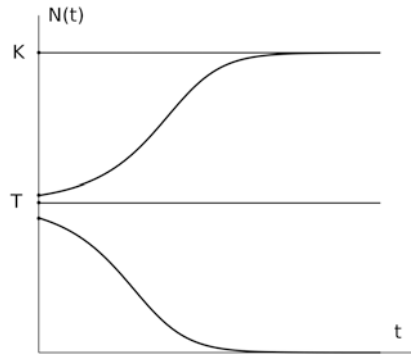


Fig. 1.12 Existence of a threshold in the strong Allee effect

is characterized by the existence of a further critical point $N = T$. Conclusions for this case are illustrated in Fig. 1.12, where we see that the population is not able to survive if its size is initially below the threshold T .

Possible polynomial forms for $r(N)$ to model the Allee effect, are

$$r(N) = r \left(1 + \frac{N}{T} \right) \left(1 - \frac{N}{K} \right) \quad (T < K), \quad (1.24)$$

for the weak effect, and

$$r(N) = r \left(\frac{N}{T} - 1 \right) \left(1 - \frac{N}{K} \right), \quad (T < K) \quad (1.25)$$

for the strong one. They are used mainly because of their simple mathematical form.

1.7 Contest and scramble competition

The logistic equation is the most used model for intraspecific competition; however other models, similar to the logistic, try to describe the mechanisms of intraspecific competition as the specific result of the nature of the interactions among individuals for resource use.

To present these models we refer to the growth rate as represented in (1.14), but focusing on the total birth rate, i.e.

$$\rho(N) = \beta(N) N.$$

We draw its shape according to two possible mechanisms describing how resources are shared among the individuals of the population.

First we consider *contest competition* that can be described in words as:

each individual needs a certain amount of resources to reproduce; when the total amount of resources is not enough for everybody (i.e. when the population abundance is above a certain threshold value) some individuals get control of the resources needed, while all the others are not able to obtain resources and cannot reproduce; thus, beyond the threshold the total birth rate is constant independently of the population size.

Alternatively we consider *scramble competition* according to the mechanism:

resources are shared equally among all individuals of the population; when this amount is insufficient for all, no individual acquires the amount of resources needed for reproduction and the birth rate drops to 0.

Both cases are shown in Fig. 1.13 where piecewise linear examples are shown, translating the two different mechanisms. Smooth versions of the same functions would be provided by assumptions such as:

$$\rho(0) = 0, \quad \rho'(x) > 0, \quad \lim_{x \rightarrow +\infty} \rho(x) = \rho_\infty < \infty; \quad (1.26)$$

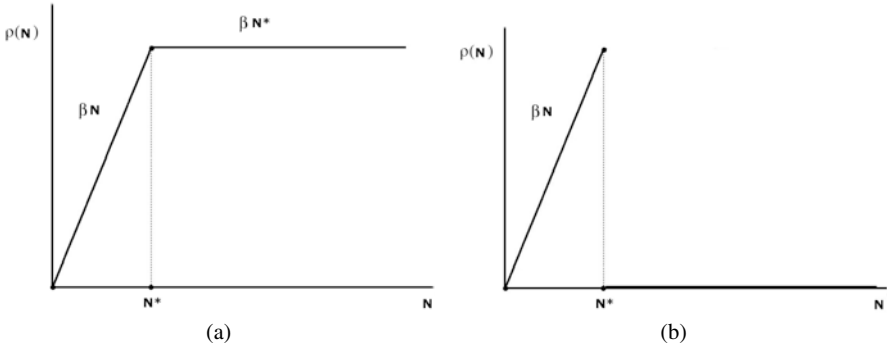


Fig. 1.13 The total birth rate $\rho(x)$ for intra-specific competition: (a) *contest competition*, individuals fight to control the amount of resources necessary to survive and reproduce; when the number of individuals is below the threshold value N^* the pro-capita growth rate is a constant β ; over this threshold, resources are sufficient to support only N^* individuals (those who win the contest) who produce βN^* newborns in the time unit; (b) *scramble competition*, individuals share resources and reproduce at a constant pro-capita rate β as far as each individual is granted the necessary amount of resources; beyond the threshold N^* the pro-capita amount is not sufficient for reproducing and there are no newborns

for the contest competition case and for scramble competition:

$$\begin{aligned} \rho(0) = 0, \quad \lim_{x \rightarrow +\infty} \rho(x) = 0 \\ \rho'(x) > 0 \quad \text{for } x < x_m, \quad \rho'(x) < 0 \quad \text{for } x > x_m \end{aligned} \quad (1.27)$$

where, in this second case, x_m is the threshold over which the total growth rate declines. Note that in both cases we have $\beta(0) = \rho'(0) > 0$ that represents the intrinsic fertility, i.e. the fertility at low population size.

Such assumptions are actually satisfied by the following parametrized forms of the growth rate

$$r(N) = \left(\frac{rK - \mu N}{K + N} \right) \quad (\text{contest competition}) \quad (1.28)$$

and

$$r(N) = \beta e^{-\nu N} - \mu \quad (\text{scramble competition}). \quad (1.29)$$

Both cases correspond to a constant mortality μ , and respective fertility

$$\beta(N) = \frac{\beta K}{K + N} \quad (\text{with } r = \beta - \mu)$$

and

$$\beta(N) = \beta e^{-\nu N}.$$

1.8 Generalist predation

Among the many factors influencing the growth of a species, we should include the interaction with other species; in particular, predators represent an additional source of mortality because they produce a direct loss of individuals. Actually, the mechanisms regulating predator-prey interaction should include a feedback effect from prey abundance on predator growth, so that a suitable framework would be a two species model. This will be treated in Part II where we will be concerned with *specialist* predation dealing with a predator essentially feeding on one single species and dying out in the absence of it. However, the case of a *generalist* predator, feeding on a wide range of preys other than the species we are interested in, may be treated in the single species framework because the abundance of the predator population would not depend on the success of predation on that single species; hence we may assume that the abundance of the predator population is independent of the size of the prey.

Thus we assume that the environment hosts a predator that has attained a stable stationary state P^* (number of individuals) and modify the models discussed in the previous sections by introducing a term to take the loss due to predation into ac-

count. The resulting model (1.15) describes a species under the influence of different effects.

The simplest constitutive form for the predation term can be derived by the *method of encounters* introduced by Volterra in [13]² and also referred as *mass action principle*. It is based on the mechanistic idea that populations act as perfect gases, completely mixed, and each individual can encounter any other individual of the population. Thus, the number of possible encounters between P^* predators and $N(t)$ preys is proportional

$$P^* \cdot N(t)$$

and, we assume:

in the unit time, a fixed fraction a of all possible encounters is effective, i.e. it ends with the killing of the prey; thus the predation term has the form

$$-aP^*N(t). \quad (1.30)$$

The parameter a is a *per-capita rate* (dimensions $[t^{-1} \cdot N^{-1}]$) called *attack rate* or *effective killing rate*.

As an example we consider the Verhulst model that with the predation term becomes

$$N'(t) = F(N(t)) = r \left(1 - \frac{N(t)}{K} \right) N(t) - aP^*N(t) \quad (1.31)$$

In this case, the growth rate has the form

$$r(N) = r \left(1 - \frac{N}{K} \right) - aP^*,$$

and the term aP^* (*predation rate*) is an extra mortality term giving the fraction of individuals dying in the unit of time, due to the predation mechanisms.

With model (1.31) we study the action of a generalist predator on a prey due to predator attacks subjected to a logistic effect. By the transformation

$$t \rightarrow \tilde{t} = rt, \quad u = \frac{N}{K},$$

we rescale the model into

$$u'(t) = F(u(t)) = (1 - u(t))u(t) - \rho u(t),$$

where $\rho = \frac{aP^*}{r}$ is a dimensionless parameter, measuring the action of the predator. We can look how the behavior of the system changes when ρ is varied, i.e. we use ρ as a bifurcation parameter (see Appendix A). Considering the steady states of the

² The celebrated model named after Volterra and Lotka will be discussed later in Chap. 6.

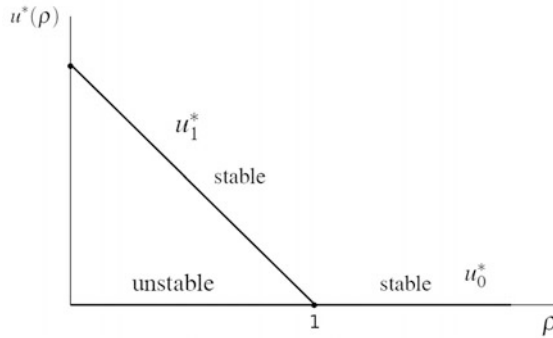


Fig. 1.14 Generalist predator: bifurcation graph for model (1.31)

system, we find the two branches

$$u_0^*(\rho) = 0, \quad u_1^*(\rho) = (1 - \rho),$$

where the non-trivial branch $u_1^*(\rho)$ is meaningful only for $\rho < 1$. Moreover, since

$$F'(u_0^*(\rho)) = 1 - \rho, \quad F'(u_1^*(\rho)) = -(1 - \rho)$$

we have the bifurcation graph shown in Fig. 1.14 where also the equilibria stability is depicted. We see that the prey is able to survive and colonize the habitat when $\rho < 1$ (the intrinsic Malthusian parameter r is greater than the predation rate aP^*) otherwise it goes extinct. Due to predation pressure $u_1^*(\rho) < 1$, i.e. the prey size at equilibrium is lower than its intrinsic carrying capacity K .

The previous model provides rather simple (even obvious and expected) conclusions on the effect of predation on a species undergoing logistic growth. We note, however, that the constitutive form (1.30), adopted to model the predation mechanisms, is not very realistic because it allows a given number of predators to kill and consume a number of preys linearly increasing with prey abundance. In reality, when preys are very abundant, there may be a saturation effect: each predator will kill and consume only a limited amount of preys. On the other hand linear dependence may be not adequate also at low prey abundance because it may not account for mechanisms through which a predator looks for its food.

The need for more suitable models leads in fact to the more general form for the rate at which preys are killed and consumed by predators

$$-\pi(N)P^*,$$

where the function $\pi(N)$ is assumed to satisfy at least the basic assumptions

$$\pi(0) = 0, \quad \pi'(N) > 0. \quad (1.32)$$

The shape of this function has been discussed by many authors and different forms have been proposed, corresponding to different modeling needs. Usually, the basic references go back to the work of C.S. Holling [6,7] and to his classification of $\pi(H)$, named *functional response*:

$$\begin{aligned}
 \text{Holling I: } \pi(N) &= \begin{cases} aN, & \text{for } N \in [0, N^*], \\ aN^*, & \text{for } N > N^*, \end{cases} \\
 \text{Holling II: } \pi(N) &= \frac{aN}{1 + a\tau N}, \\
 \text{Holling III: } \pi(N) &= \frac{\alpha N^\theta}{v^\theta + N^\theta}, \quad \text{with } \theta > 1,
 \end{aligned} \tag{1.33}$$

where the different parameters have different meaning and dimensions. In types *I* and *II*, $a > 0$ is the *attack rate* with the same meaning as in (1.30). In type *II*, $\tau > 0$ is the *time to consume one captured prey* and is related to the *maximum killing rate* α (i.e. the number of preys killed in the time unit by one predator, when the prey abundance is extremely large) by

$$\alpha = \pi(+\infty) = \frac{1}{\tau}.$$

Actually, in this case the form of $\pi(H)$ can be derived introducing τ into the mechanism of encounters (see [7]). In fact, during a given length of time Δt , one predator, kills $\pi(H)\Delta t$ preys and spends the time $\tau\pi(H)\Delta t$ to consume them; hence the preys it kills must be killed during the remaining time $(\Delta t - \tau\pi(H)\Delta t)$. Thus

$$\pi(H)\Delta t = aH(\Delta t - \tau\pi(H)\Delta t)$$

from which *Holling II* form is derived.

In type *III* the parameter α appears explicitly, while v has the same dimensions as the number of individuals and is such that

$$\pi(v) = \frac{1}{2}\alpha.$$

This form of $\pi(H)$ has not a mechanistic explanation as in the case of type *II* but is justified empirically on the basis of field data. Type *I* is in fact a rough modification of the one we have already considered, based on mass action and the principle of encounters, while types *II* and *III*, both satisfying (1.32), are considered more realistic and are respectively called (see Fig. 1.15) *hyperbolic response* and *sigmoidal response*. In the latter the exponent θ may be set and justified in terms of the predation mechanism and its role consists in a reduction of predation at low prey density, as it is the case of a generalist predator that, having other food sources, does not care

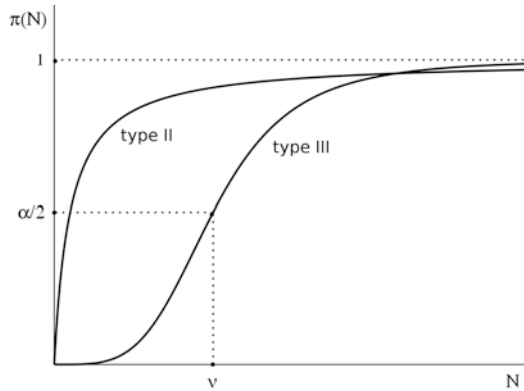


Fig. 1.15 Hyperbolic and sigmoidal responses compared

of the prey until it is abundant enough to be “visible”. Thus, a functional response of type *Holling III* (with $\theta = 2$), is especially suitable for the case of a generalist predator and the model becomes

$$N'(t) = r \left(1 - \frac{N(t)}{K} \right) N(t) - \frac{\alpha P^* N^2(t)}{v^2 + N^2(t)}, \quad (1.34)$$

This model is rather rich and has been used to model the specific case of the *spruce-budworm* ecosystem that will be analyzed in the next section.

Dimensions and scaling

As we have seen in the previous pages, the basic variables intervening in the modeling of homogeneous populations are the number of individuals and time. The respective units they are measured with form a dimensional system $[N, t]$ from which all other parameters depend. Thus the growth rate, measuring the number of new individuals per individual in the unit of time, has dimensions $[t^{-1}]$, which are also the dimensions of the functional response $\pi(N)$. As for the parameters appearing in the different explicit forms of $\pi(N)$, the attack rate α has dimensions $[N^{-1} \times t^{-1}]$ while α and v respectively have dimensions $[t^{-1}]$ and $[N]$.

In the practice of dimensional analysis of mathematical models, it is often convenient to group different parameters into dimensionless parameters and possibly to reduce their number. This procedure of scaling the variables, may lead to identify meaningful parameters such as R_0 , introduced in (1.6), or to simplify the equations as in (1.22) and help the analysis. Moreover, grouping and reducing, relevant bifurcation parameters may be obtained in order to more effectively discuss the model.

The procedure of scaling is however not univocal and it should be guided by the specific purposes of the analysis we wish to perform. The case of model (1.31) and of the spruce-budworm model are good examples of the concepts introduced above.

1.9 The spruce-budworm system

The spruce-budworm dynamics concerns the ecological case study of the interaction between the spruce-budworm and the balsam-fir forests in Eastern North America. The spruce-budworm is in fact one of the insect pests affecting vegetation, through periodic outbreak that represent a great concern for forest conservation. Apart from extensive qualitative studies, the spruce-budworm has been the object of a detailed modeling effort, in order to identify mechanisms apt to explain the dynamics. In [8], model (1.34) is assumed as representative of the ecosystem to provide an insight into its qualitative behavior.

Model (1.34) is adopted after identifying the abundance $N(t)$ of the budworm as the only *fast* variable of the ecosystem. Instead, the carrying capacity K , depending on the amount of foliage of the forest, is identified as a *slow* variable, hence with respect to the fast scale it can be approximated as a constant. On the other hand, the predator population, whose action is exerted at the same time scale of the budworm, is not a dynamic variable because the predator is generalist and its abundance is also a constant of the model. Finally, the functional response of predation is given the phenomenological form of type Holling III, again because the predator is generalist and the response is low for low prey abundance.

In order to analyze model (1.34), we first scale the variables adopting a new time unit $\tau = \frac{v}{\alpha P^*}$ and performing the transformations

$$t \rightarrow \tilde{t} = \frac{t}{\tau}, \quad N \rightarrow u = \frac{N}{v}$$

we then obtain the equation

$$u'(t) = F(u(t)) = \left[\rho \left(1 - \frac{u(t)}{q} \right) - \frac{u(t)}{1 + u^2(t)} \right] u(t) \quad (1.35)$$

with the dimensionless parameters

$$\rho = \frac{r_0 v}{\alpha P^*}, \quad q = \frac{K}{v}.$$

A main feature of model (1.34) is that the trivial extinction equilibrium $u^* = 0$ is unstable, since we have $F'(0) = \rho > 0$. Concerning existence of non trivial steady states, we adopt ρ as a significant parameter to vary and build a bifurcation graph to

trace non-trivial solutions of the equation

$$\rho \left(1 - \frac{u}{q} \right) - \frac{u}{1+u^2} = 0 \quad (1.36)$$

versus ρ . We may proceed graphically, looking for the intersections of the two curves

$$f(u) = \rho \left(1 - \frac{u}{q} \right), \quad g(u) = \frac{u}{1+u^2}. \quad (1.37)$$

In fact the second curve does not depend on ρ and the first one is a line whose intercept with the u -axis is fixed ($u = q$) and the intercept at $u = 0$ is exactly ρ .

Thus by Fig. 1.16 we can understand how the number of equilibria varies with ρ , in the two cases q small and q large. As it is clear from the figure, if q is too small there exists one and only one non-trivial equilibrium for any $\rho > 0$ (panel (a)); instead, if q is sufficiently large we have the situation shown in panel (b), leading to the bifurcation graph of Fig. 1.17a.

Figure 1.17b shows the shape of the growth rate of the dimensionless eq. (1.35)

$$r(u) = \rho \left(1 - \frac{u(t)}{q} \right) - \frac{u(t)}{1+u^2(t)},$$

changing as ρ crosses ρ_1 and ρ_2 .

We note that the bifurcation curve in Fig. 1.17a, implicitly defined through eq. (1.36), can be made explicit with respect to ρ as a function of the size u^* of the steady state, obtaining

$$\rho(u^*) = \frac{q u^*}{(1+u^{*2})(q-u^*)}.$$

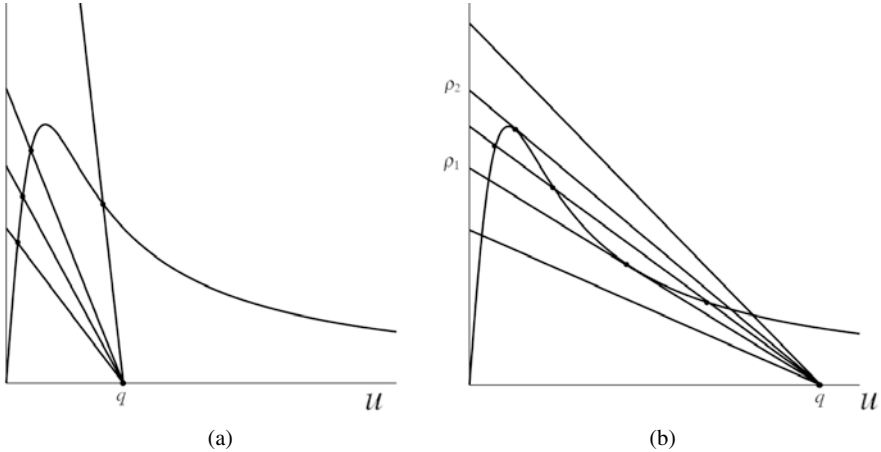


Fig. 1.16 Graphical procedure for determining non trivial equilibria of model (1.34). (a) the case of q too small when a unique equilibrium exists; (b) the case of q large enough and the existence of multiple equilibria

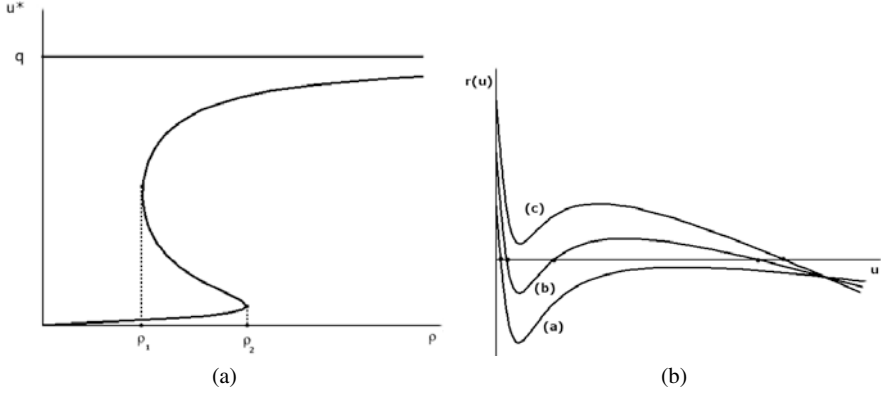


Fig. 1.17 Bifurcation of equilibria for model (1.34): (a) the bifurcation graph showing existence of multiple equilibria for $\rho \in (\rho_1, \rho_2)$; (b) the growth rate 1.36 in three different cases (a), (b) and (c) respectively corresponding to $\rho < \rho_1$, $\rho \in (\rho_1, \rho_2)$ and $\rho > \rho_2$

From the same Fig. 1.16 we can determine the stability of the states shown in Fig. 1.17. In fact, in Fig. 1.17a we identify three branches of steady states

$$\begin{aligned} u_1^*(\rho) & \text{ for } \rho \in [0, \rho_2], \\ u_2^*(\rho) & \text{ for } \rho \in (\rho_1, \rho_2), \\ u_3^*(\rho) & \text{ for } \rho \in [\rho_1, +\infty) \end{aligned}$$

satisfying

$$0 < u_i^*(\rho) < K, \quad i = 1, 2, 3,$$

$$u_1^*(\rho) < u_2^*(\rho) < u_3^*(\rho), \text{ for } \rho \in (\rho_1, \rho_2).$$

Remember that

$$F(u) = r(u) = (f(u) - g(u))u,$$

so that

$$F'(u_i^*(\rho)) = r'(u_i^*(\rho))u_i^*(\rho).$$

Now, the branch $u_1^*(\rho)$ is stable because in a neighborhood of it we have

$$g(u) < f(u) \text{ if } u < u_1^*(\rho)$$

and

$$g(u) > f(u) \text{ if } u > u_1^*(\rho)$$

so that $F'(u_1^*(\rho)) = r'(u_1^*(\rho))u_1^*(\rho) < 0$. Similarly we can show that $u_2^*(\rho)$ is unstable and $u_3^*(\rho)$ is stable.

This model may be considered a basic example for explaining catastrophic events that may occur in nature. To illustrate this occurrence (see Fig. 1.18) we start considering an intrinsic growth rate $\rho \in (0, \rho_1)$. Such a value corresponds to the existence of a unique equilibrium $u_1^*(\rho)$ that, being stable, attracts any solution and we can

assume that the ecosystem described by the model, has attained such a state. Let now ρ have a small increase (due for instance to habitat changes or to some intrinsic variation of the species) to a new value $\bar{\rho}$ still less than ρ_1 . We expect the ecosystem to be driven to the new equilibrium $u_1^*(\bar{\rho})$ (greater than the previous one). In fact, as it is shown in Fig. 1.18-(a), after ρ has increased to $\bar{\rho}$, we can think of the previous equilibrium $u_1(\rho)$ as an initial condition for the new system and the new equilibrium $u_1(\bar{\rho})$ attracts the solution: the ecosystem attains a new equilibrium. The same change occurs for further increases of ρ , even if ρ crosses the value ρ_1 . In fact, in this case (see Fig. 1.18-(b)), even though two new equilibria appears after the change of ρ , the previous equilibrium belongs to the basin of attraction of the new $u_1^*(\bar{\rho})$. A different event (Fig. 1.18-(c)) occurs when, by a further increase, ρ crosses ρ_2 since in this case the unique new equilibrium $u_3^*(\bar{\rho})$ attracts the trajectory starting from a “far away” previous equilibrium $u_1^*(\rho)$. Afterwards, even though we may try to draw

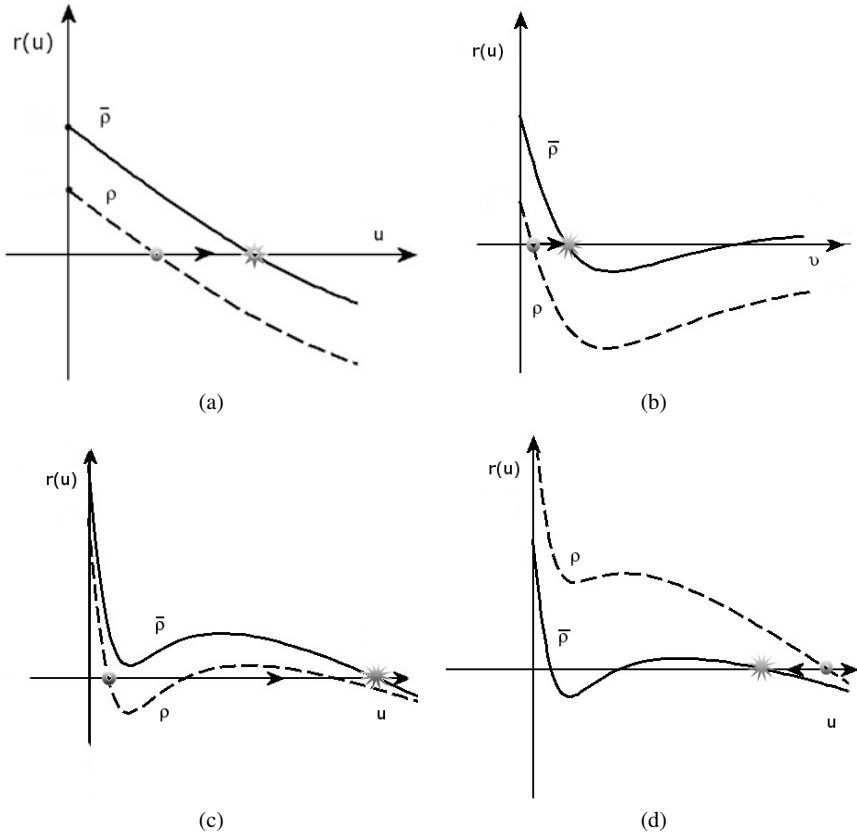


Fig. 1.18 The effect of environmental changes on the spruce-budworm dynamics: (a) for $\rho < \bar{\rho} < \rho_1$, the previous equilibrium $u_1^*(\rho)$ switches to $u_1^*(\bar{\rho})$; (b) $\rho < \rho_1 < \bar{\rho}$, again the system switches from $u_1^*(\rho)$ to $u_1^*(\bar{\rho})$; (c) $\rho < \rho_2 < \bar{\rho}$, the system switches from $u_1^*(\rho)$ to $u_3^*(\bar{\rho})$; (d) when $\bar{\rho} < \rho_2 < \rho$, the system switches from $u_3^*(\rho)$ to $u_3^*(\bar{\rho})$

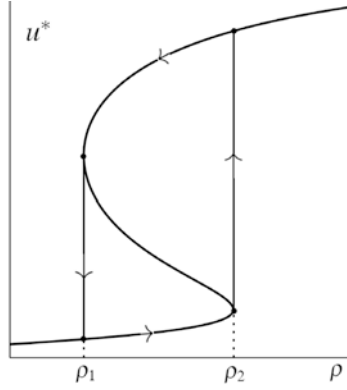


Fig. 1.19 The hysteresis cycle possibly run by the spruce-budworm system under the influences of habitat changes

back the system to the previous equilibrium, driving ρ to a value $\bar{\rho} < \rho_2$, we cannot reach back $u_1^*(\bar{\rho})$, but the system will attain $u_3^*(\bar{\rho})$, as it is shown in Fig. 1.18-(d). A further decrease of ρ below ρ_1 will necessary for the system to go back to $u_1^*(\rho)$.

On the whole, under the influence of habitat changes described above, the system would follow a kind of hysteresis cycle which is shown in Fig. 1.19.

1.10 Harvesting

Fishing, hunting and all that are of course a kind of predation, but we call it harvesting because it is performed by mankind. Modeling of the ecosystem is important to evaluate the effect of such an action, both for knowing the limits we have to observe to prevent the extinction of the population, and for designing the optimal strategy providing the maximum yield. Actually, a significant model for analyzing harvesting may be model (1.31) where the term (1.30), instead of predation, now describes the subtraction of individuals due to harvesting. Thus (1.31) can be rephrased as

$$N'(t) = F(N(t)) = r \left(1 - \frac{N(t)}{K} \right) N(t) - hE N(t) \quad (1.38)$$

where E measures the *effort*, i.e. the energy spent per unit of time, and h measures the *return*, i.e. the fraction of the population, harvested per unit of effort.

We are basically interested in:

- determining within which range we can exert the effort, without destroying the population;
- determining the effort corresponding to the maximum yield.

Under the pressure of harvesting, that we suppose exerted at all times, the ecosystem is perturbed and switches to some steady state compatible with harvesting. This will depend on the effort itself, and a first task is to understand how steady states depend on E .

In the case of model (1.38) there are the following equilibria, expressed as functions of E ,

$$N_0^*(E) \equiv 0, \quad N_1^*(E) = \left(1 - \frac{hE}{r}\right) K$$

which lead to the bifurcation graph shown in Fig. 1.14. Thus we see that, in order to preserve the population from extinction, it must be $0 \leq E < \frac{r}{h}$.

When the system has attained the non trivial steady state $N_1^*(E)$, the total yield in unit time, as a function of the effort E , is

$$Y(E) = hEN_1^*(E) = hE \left(1 - \frac{hE}{r}\right) K.$$

Finding the maximum of $Y(E)$, we easily see that the optimal effort and the maximum yield are, respectively,

$$E_{max} = \frac{r}{2h}, \quad Y(E_{max}) = \frac{rK}{4}.$$

The previous example is somewhat typical of the harvesting of a population undergoing some logistic effect. In the general case of model (1.15) we have to solve

$$r(N) - hE = 0,$$

to represent the perturbed steady states as functions of E and compute the corresponding yield $Y(E)$.

Note that the economic theory does not at all predict that the optimal effort E_{max} will be reached. An application of the so called *open-access* theory is given in the problems. Furthermore, recurrent crashes in fished populations witness for lack of an optimal harvesting policy.

The problems presented in this section conjugate Ecology and Economics. A basic treatise on the subject is the book by C.W. Clark [2], dedicated to the mathematical modeling of the complex problems of bioeconomics.

Problems

1.1. Fitting data

Population data such as those presented in Table 1.1 can be found on the web at the address

<http://www.census.gov/ipc/www/idb/>

where population data of all countries are regularly published.

1. Go to the site mentioned above and look for data relative to different countries to perform exponential fits using computer packages.
2. Since the exponential fit may be not satisfactory try to fit only part of the data.
3. If the exponential fit is not satisfactory, try to fit the same data by a logistic curve.

This can be done from (1.21) that gives

$$\ln \left(\frac{1}{N(t)} - \frac{1}{K} \right) = -rt + \ln \left(\frac{1}{N_0} - \frac{1}{K} \right).$$

In fact after a guess of K you can determine the other parameters by an exponential fit of the transformed data N_i into

$$Z_i = \ln \left(\frac{1}{N_i} - \frac{1}{K} \right).$$

4. In order to guess K in the previous point you can take the values of $N(t)$ at three different times $t_1 = \tau$, $t_2 = 2\tau$, $t_3 = 3\tau$. Namely, if $N(\tau) = n_1$, $N(2\tau) = n_2$, $N(3\tau) = n_3$, then the carrying capacity is

$$K = \frac{1/n_1 + 1/n_3 - 2/n_2}{1/(n_1 n_3) - 1/n_2^2}.$$

Prove this formula and use it in the previous point.

1.2. Exogenous variability

Consider the time dependent Malthus model (1.10) with periodic Malthus parameter:

$$r(t+T) = r(t)$$

and take the average over one period

$$\bar{r} = \frac{1}{T} \int_0^T r(s) ds.$$

1. After showing that the function

$$\pi(t) = \int_0^t r(s) ds - \bar{r}t \tag{1.39}$$

is periodic with period T , prove (1.12) and (1.13).

2. Introduce in (1.10) a term representing time dependent immigration

$$N'(t) = r(t)N(t) + m(t), \quad (1.40)$$

assuming both $r(t)$ and $m(t)$ periodic with period T . Using (1.39), show that, if $\bar{r} < 0$, then the function

$$N_\infty(t) = \int_{-\infty}^t e^{\int_s^t r(\sigma) d\sigma} m(s) ds$$

is well defined, is a solution to (1.40) and is periodic with period T .

3. Show that if $\bar{r} < 0$, then the solution to (1.40) with initial condition N_0 ,

$$N(t) = e^{\int_0^t r(\sigma) d\sigma} N_0 + \int_0^t e^{\int_s^t r(\sigma) d\sigma} m(s) ds,$$

has $N_\infty(t)$ as its asymptotic limit, i.e.

$$\lim_{t \rightarrow +\infty} (N(t) - N_\infty(t)) = 0.$$

1.3. Intraspecific competition

Assume that the growth rate of a population depends on *available* resources $\rho(t)$, according to a general law

$$r(t) = G(\rho(t)).$$

Assume for the moment that the total amount of resources is a fixed constant C , but they can be *free* (hence available, denoted by $\rho(t)$) or *used by the population*, denoted by $H(N(t))$, where dependence on the population is shown. In other words

$$\rho(t) = C - H(N(t)), \quad (1.41)$$

and the resulting model

$$N'(t) = G(C - H(N(t)))N(t) \quad (1.42)$$

will be specified when the functions $G(\cdot)$ and $H(\cdot)$ are given.

1. Explain why reasonable assumptions are that both G and H are increasing functions with $G(0) < 0$, $H(0) = 0$.
2. Choose a linear form for G and H and show that the growth rate has the form (1.19).
3. With the previous assumptions, does eq. (1.42) always have a positive equilibrium? If not, find the conditions under which it does and find the expressions for the intrinsic rate of growth r and the carrying capacity K .
4. Using generic functions G and H satisfying the assumptions of point 1, find under which conditions the eq. (1.42) has a unique positive equilibrium. When is it asymptotically stable?
5. What could be other reasonable assumptions for ρ instead of (1.41)?

1.4. Sexual reproduction

It may be considered reasonable that, for a sexual species, births are proportional to the number of encounters, hence, disregarding the mortality process:

$$N'(t) = \beta N^2(t).$$

1. Show that the solutions of this equation with $N(0) > 0$ tend to infinity in a finite time.
2. Let us correct the equation, introducing deaths:

$$N'(t) = \beta N^2(t) - \mu N(t).$$

Discuss how the dynamics changes. In particular, does the equation still have the problem of solutions going to infinity in a finite time?

3. Let us introduce a limiting factor of logistic type:

$$N'(t) = (\beta N^2(t) - \mu N(t)) (1 - \gamma N(t)).$$

Show that for $N_0 > 0$ a global solution of the problem exists. Find all non-negative equilibria and discuss their stability.

1.5. Generalist predation

Different models arise when combining different forms of the prey growth rate with different functional responses. In sections 1.8 and 1.9 we have analyzed two cases, but there are more. The graphical procedure to determine equilibria can be used in the analysis, choosing suitable functions to work with.

1. Consider again problem (1.34) and look for equilibria, as ρ varies, adopting the functions

$$f(u) = (q - u)(1 + u^2), \quad g(u) = \frac{q}{\rho}u,$$

instead of (1.37).

2. In the previous item find the value \bar{q} such that for $q < \bar{q}$ there is a unique equilibrium (panel (a) of Fig. 1.16) for all values of ρ , and for $q > \bar{q}$ multiple equilibria occur for some values of ρ (panel (b) of the same figure).
3. Consider the case of a generalist predator with functional response of type *Holling II* and a prey undergoing logistic growth; choose significant parameters and discuss the relative bifurcation graph.
4. Consider a prey with a weak Allee effect, modeled by (1.24), and a generalist predator with a linear functional response.
5. Study the same prey as in the previous item but with a predator with functional response *Holling II*.
6. Repeat the study of the previous item with a functional response *Holling III*.
7. Consider the case of a prey with strong Allee effect, modeled by (1.25), and a generalist predator with the three functional responses considered in the previous items.

1.6. Harvesting problems

Let us consider a population growing according to a logistic dynamics. Let assume that a constant effort E of fishing³ is exerted so that the yield per unit time is $hEN(t)$, where $N(t)$ is the population size and h is a coefficient denoting the return to effort.

1. Let assume that the unit price at which the fish is sold is p , and that the cost of fishing is proportional (through a coefficient c) to the effort E . Suppose we want to follow an optimal harvesting strategy setting E at the value that maximizes the gain (= revenue – cost) when the population is at its asymptotically stable equilibrium. Find the value of E and the corresponding equilibrium value for N .
2. Economic theory predicts that, for an *open access* fishery, the effort E will in the long run reach the value at which the gain is equal to 0. Assuming that this actually happens, find the value of E and the corresponding equilibrium value of N ; compare them (i.e, find, if they are greater or smaller) to those in the previous case.
3. Let assume that the government taxes at a percentage θ the gains obtained by fisheries. How does this affect the results obtained with open-access fishery?
4. Consider again open-access fishery and assume that the government taxes according to how much has been fished Y . Let us consider two separate cases: a constant fraction θY , or a progressive tax $\tau(Y)$ given by the formula

$$\tau(Y) = \begin{cases} 0 & \text{if } Y \leq Y_0 \\ \theta(Y - Y_0) & \text{if } Y > Y_0 \end{cases}$$

Which are the results of these regulations?

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³ or hunting, or harvesting.

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Population models with delays

Una notte osservavo come al solito il cielo col mio telescopio. Notai che da una galassia lontana cento milioni d'anni-luce sporgeva un cartello. C'era scritto: TI HO VISTO. Feci rapidamente il calcolo: la luce della galassia aveva impiegato cento milioni di anni a raggiungermi e siccome di lassù vedevano quello che succedeva qui con cento milioni d'anni di ritardo, il momento in cui mi avevano visto doveva risalire a duecento milioni d'anni fa.¹

*Italo Calvino, "Gli anni luce"
in "Le Cosmicomiche", 1965*

The possibility that events, lost in the past, still influence our lives, is an evocative notion, strongly inspiring literature, at least. The character of the tale by Italo Calvino, quoted in the foreword, is in fact obsessed by some event happened millions of years before, within an hallucinatory mixture of space and time. However, the need of including the influence of past effects in the description of natural phenomena was explicitly recognized by Vito Volterra in a lecture in 1912 ([8]), where we read²:

at this point we may ask if natural phenomena really occur in such a way, or else we have to suppose that there effectively exists an heredity of past events, so that disregarding such heredity represents an approximation introduced only for study convenience.

Though at that time Volterra was not yet involved in population dynamics, later he discussed the introduction of past history in his celebrated predator-prey model (see Chap. 6 and [9]).

Indeed nowadays, delay differential equations and integro-differential equations of Volterra type (also classified as *concentrated* delay and *distributed* delay equations, respectively) are important chapters of the theory of differential equations and their interest has been especially enhanced because of models in population dynam-

¹ One night I was, as usual, observing the sky with my telescope. I noticed that a sign was hanging from a galaxy a hundred million light-years away. On it was written: I SAW YOU. I made a quick calculation: the galaxy's light had taken a hundred million years to reach me, and since they saw up there what was taking place here a hundred million years later, the moment when they had seen me must date back two hundred million years. (Translation by William Weaver)

² Vito Volterra considerations actually concern the concept of *functions that depend on other functions* that may be considered as a first step toward Functional Analysis.

ics. In fact, after Volterra's ansatz, the need of taking into account the *hereditary* nature of population phenomena was pointed out since the very beginning of the mathematical modeling of population growth, and some attention has been devoted to the specific mechanisms that ask for the introduction of delays into the equations. The next section provides a short discussion to the modeling aspect of the problem, then we will consider the delayed Malthus and Verhulst models both in the concentrated case and in the distributed one. The following section is devoted to age structure as a source of delays.

This chapter requires a more advanced mathematics than the previous one and some basic theory is presented in Appendix B. Our aim here is to show how delays endow models of population growth with new properties and how to use the methods needed. More technical computations are left to a final section.

2.1 Why delays, and how

When trying to describe the status of an ecosystem at a certain time, we should be aware of the fact that some of the mechanisms involved in the dynamics may depend on the status of the population at past times, more than at present. First, we note that reproduction must reflect the status of the population at some moment in the past, since *gestation times* imply that present birth rates must depend on the number of individuals at fecundation more than those at present. A more general reason for considering delays is that some of the habitat features influencing population growth at a given time may be influenced by the population abundance in the past.

To discuss the introduction of gestation times we modify the simple Malthus model by taking into account a gestation time, assumed to be a constant τ . We base our model on four parameters:

- ϕ : the rate at which individuals become pregnant;
- ν : the average number of newborns from a pregnant individual;
- τ : gestation length;
- μ : mortality.

Computing birth and death rates, one immediately obtains the equation

$$N'(t) = kN(t - \tau) - \mu N(t) \quad (2.1)$$

where

$$k = \nu\phi e^{-\mu\tau}.$$

In fact, at time t , we have ν newborns, coming from each individual who had become pregnant at time $t - \tau$ and is still alive at time t , with survival probability $e^{-\mu\tau}$, through the gestation time (see (1.5)).

Thus, the parameter k in eq. (2.1), that at first sight may be considered a fertility rate (as in the original Malthus model), actually combines all four biological parameters listed above.

In the same spirit, nonlinear models with gestation time can be derived from the examples considered in Sect. 1.7, starting with the total birth rate $\rho(N)$. In fact, the same argument leads to models in which the reproduction process depends on population abundance at a previous time

$$N'(t) = e^{-\mu\tau} \rho(N(t - \tau)) - \mu N(t) \quad (2.2)$$

where, again, the factor $e^{-\mu\tau}$ takes into account the probability of surviving pregnancy. In principle, one may allow also for mortality to depend on population size, but this would make the model more complex, since the nonlinearity should be considered also in the computation of the probability of surviving pregnancy. Concerning the fertility function $\rho(x)$, if we compare the two cases of contest and scramble competition, we see that the results in terms of equilibrium stability are rather different.

A dataset that has been widely analyzed in this context is one reported by Nicholson [6]: the dynamics in laboratory of a population of blowflies over a period of nearly two years that displays rather wide and regular oscillations. Such behavior is compatible with the properties of several models discussed in this chapter (see the analysis in the following sections). It is now generally accepted that a model like (2.2) based on development delays with a function $\rho(x)$ with a shape such as that corresponding to scramble competition is more adequate for that specific case-study than a model like (2.3) based on delayed effects on growth rates.

A very influential example of delay differential equations was proposed by Hutchinson in [4], who modified the Verhulst model by inserting a time-lag in the growth rate. Namely, the standard logistic model is modified into the equation

$$N'(t) = r \left(1 - \frac{N(t - \tau)}{K} \right) N(t). \quad (2.3)$$

The idea is that, since the habitat needs a certain time (here represented by τ) to recover after exploitation (or, more in general, since the logistic effect is not instantaneous), the reduction of the growth rate at time t depends on the status of the population (i.e on the number of individuals) at time $t - \tau$. Indeed, such an argument is rather phenomenological and does not refer to any specific mechanisms concerning the variations of the habitat under population pressure. Despite these limitations, model (2.3) has been widely used to explore the effect of generic delayed responses on the growth of a population; eq. (2.3) is simple and representative of a class of models including delays in the per-capita growth rate.

Model (2.3) is an equation with concentrated delays, but similar models with distributed delays have also been considered (see [3]), such as

$$N'(t) = r \left(1 - \gamma N(t) - \eta \int_{-\infty}^t K(t-s) N(s) ds \right) N(t). \quad (2.4)$$

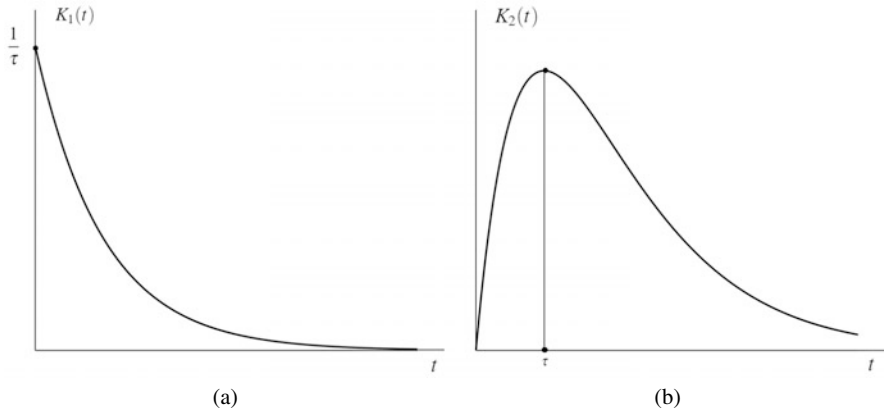


Fig. 2.1 The memory kernels of (2.5): (a) the fading memory kernel $K_1(t)$; (b) kernel $K_2(t)$ with memory concentrated at $t = \tau$

Here, instead of referring to a fixed lag of time, we have a spanning effect through a memory kernel $K(t)$ that weighs the impact of the population presence through its whole past history; moreover, the parameter γ weighs also the impact of the present population.

Examples of kernels $K(t)$ that have been extensively used (mainly for mathematical reasons, as will be seen in next sections) are

$$K_1(t) = \frac{1}{\tau} e^{-\frac{t}{\tau}}, \quad K_2(t) = \frac{t}{\tau^2} e^{-\frac{t}{\tau}}. \quad (2.5)$$

The kernel $K_1(t)$ is decreasing and represents a *fading memory*, while $K_2(t)$ introduces a memory peaking at $t = \tau$ (see Fig. 2.1). Both kernels are normalized

$$\int_0^{\infty} K_i(t) dt = 1, \quad i = 1, 2.$$

In all the equations considered in this chapter, in order to have a solution from time $t = 0$ onwards, one needs to assign, as an initial condition, a past history of the system. Specifically, in (2.1) and (2.3) one has to assign

$$N(t) = \phi(t), \quad t \in (-\tau, 0]. \quad (2.6)$$

In (2.4), with kernels such as K_1 or K_2 , the initial condition must be

$$N(t) = \phi(t), \quad t \in (-\infty, 0]. \quad (2.7)$$

2.2 Analysis of the delayed Malthus model

Let us consider eq. (2.1), which is linear, and analyze the structure of the solution and its behavior. Namely, as explained in Appendix B, we aim at an asymptotic expansion of the solution through a series of particular solutions of exponential type

$$N(t) \approx \sum_{j=0}^{+\infty} c_j e^{\lambda_j t}, \quad (2.8)$$

where $e^{\lambda_j t}$ are exponential solutions of (2.1) while c_j are constants depending on the initial heredity (the function $\phi(t)$ in (2.6)). Substituting $e^{\lambda_j t}$ in (2.1), we see that this will be a solution if and only if λ_j is a solution of the characteristic equation

$$\lambda + \mu = k e^{-\tau \lambda}. \quad (2.9)$$

Note that if $\tau = 0$ such equation becomes (in this case $k = \beta$)

$$\lambda = \beta - \mu$$

and there is only one root, producing the unique solution $N(t) = N_0 e^{(\beta - \mu)t}$ of the non delayed Malthus model.

On the other hand, if $\tau > 0$, eq. (2.9) has a sequence of roots in the complex plane whose location we need to determine. In fact we have that:

eq. (2.9) has one and only one real solution $\lambda_0 = \alpha^*$. If λ_i is any other root of (2.9) then

$$\Re \lambda_i < \alpha^*.$$

The proof of this fact, as well as that of a more technical property of solution of (2.9) is delayed to the final section of this chapter, devoted to the analysis of characteristic equations of this type. However, based on this result, we know that α^* is the leading root in the expansion (2.8) so that we have

$$N(t) = c_0 e^{\alpha^* t} (1 + \Omega(t)), \quad \lim_{t \rightarrow +\infty} \Omega(t) = 0 \quad (2.10)$$

showing that the ultimate behavior of $N(t)$ is exponential in time, as in Malthus model, with an exponent α^* .

One can also extend formula (2.10) by including other terms. Indeed, it can be proved that there is a unique pair of conjugate roots $\lambda_{1,2} = \alpha_1 \pm i\omega_1$ such that $\Re \lambda_j < \alpha_1 < \alpha^*$ for any other root λ_j . Now the terms $e^{(\alpha_1 \pm i\omega_1)t}$ both involve linear combinations of $e^{\alpha_1 t} \cos(\omega_1 t)$ and $e^{\alpha_1 t} \sin(\omega_1 t)$. Through some simple steps, one can then arrive at the expansion

$$N(t) = c_0 e^{\alpha^* t} \left(1 + \kappa_1 e^{(\alpha_1 - \alpha^*)t} \cos(\omega_1 t) + \kappa_2 e^{(\alpha_1 - \alpha^*)t} \sin(\omega_1 t) \right) (1 + \Omega(t)) \quad (2.11)$$

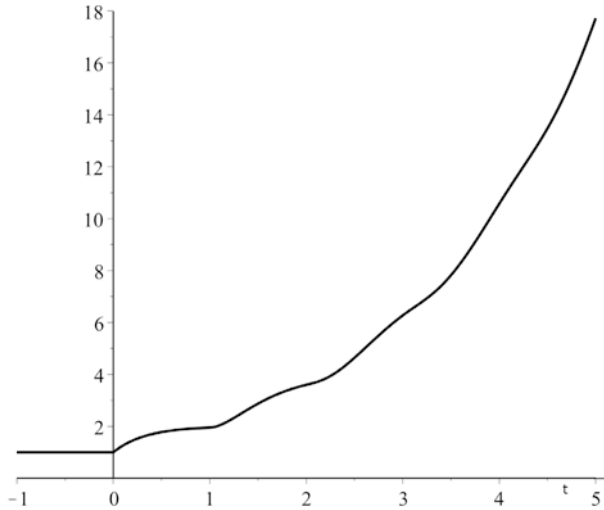


Fig. 2.2 The solution of model 2.1 with $\tau = 1$, $k = 6$, $\mu = 3$ and $\phi(t) = 1$, $t \in [-1, 0]$. The solution can be explicitly computed by the method of steps (see Problem 2.2). Oscillations occur even though the initial heredity is constant

where $\lim_{t \rightarrow +\infty} \Omega(t) = 0$. This shows that, beyond the dominant exponential term, there are sub-dominant oscillatory terms that can be seen in numerical solutions of (2.1). A solution is in fact shown in Fig. 2.2, where vanishing oscillations occur to perturb a mainly exponential behavior.

The leading root α^* can be easily computed numerically. In order to have some analytical grasp on its value, Fig. 2.7 shows that α^* has the same sign as $k - \mu$. Noting that the reproduction number in the delayed model (2.1) is equal to

$$R_0(\tau) = \frac{k}{\mu} = \frac{\beta e^{-\mu\tau}}{\mu} \quad (2.12)$$

where we show dependence on τ , the previous observation on the sign of α^* can be rephrased as:

$$\alpha^* < 0 \quad (\text{resp. } > 0) \quad \text{if and only if} \quad R_0(\tau) < 1 \quad (\text{resp. } > 1).$$

Note that $R_0(0) = \frac{\beta}{\mu}$ as in the Malthus model (see (1.6)) and $R_0(\tau)$ is decreasing as the delay increases. Thus we may infer that in this model, long gestation times may lead the population to extinction, and more generally decrease the growth rate of the population.

2.3 Analysis of nonlinear models with delay

We now consider the non-linear delayed logistic model (2.3). First of all, we rescale the equation by the transformation

$$t \rightarrow \tilde{t} = rt, \quad \tau \rightarrow \tilde{\tau} = r\tau, \quad N \rightarrow u = \frac{N}{K}.$$

This leads (renaming \tilde{t} and $\tilde{\tau}$ as t and τ) to the equation

$$u'(t) = (1 - u(t - \tau))u(t), \quad (2.13)$$

with only one dimensionless parameter τ .

We start by finding the steady states of (2.13), namely the constant solutions $u(t) \equiv u^*$, satisfying

$$(1 - u^*)u^* = 0.$$

Indeed we have the same steady states of the non-delayed logistic equations

$$u^* = 0, \quad u^* = 1.$$

Then we discuss their stability by linearizing (2.13). We get the following two equations for the deviation $\omega(t) = u(t) - u^*$ (see Appendix B)

$$\begin{aligned} \text{at } u^* = 0, \quad \omega'(t) &= \omega(t); \\ \text{at } u^* = 1, \quad \omega'(t) &= -\omega(t - \tau). \end{aligned}$$

Looking, as in the previous section, for exponential solutions $e^{\lambda t}$, we obtain the respective characteristic equations

$$\lambda = 1, \quad (2.14)$$

$$\lambda = -e^{-\tau\lambda}. \quad (2.15)$$

Equation (2.14) shows that $u^* = 0$ is unstable, in fact the solutions of the linearized equation are $\omega(t) = \omega_0 e^t$, meaning that deviations tend to grow exponentially. As for eq. (2.15), in Sect. 2.6 we prove that:

if τ is sufficiently small, all the roots of (2.15) have negative real part.

Thus, for τ sufficiently small, the steady state $u^* = 1$ is asymptotically stable, since all roots of (2.15) are in the left hand side of the complex plane.

In order to understand what happens for larger τ , we study how the location of roots of (2.15) changes with τ . From the analysis of the change in the location of roots, reported at the end of this chapter in Sect. 2.6 and displayed graphically in Fig. 2.3, it is possible to conclude that at $\tau = \frac{\pi}{2}$ two complex conjugate roots of (2.15) cross the imaginary axis so that the equilibrium solution $u^* = 1$ becomes unstable.

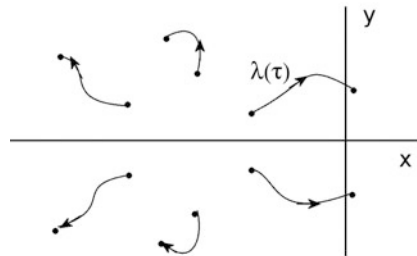


Fig. 2.3 The roots of (2.15) in the complex plane as τ varies. At $\tau = \frac{\pi}{2}$ Hopf bifurcation occurs when two complex roots cross the imaginary axis

This result is a *prelude to Hopf bifurcation* as discussed in Appendix A; numerical evidence shows that Hopf bifurcation actually occurs. In conclusion, summarizing all results we have that:

the extinction state $u^* = 0$ is unstable, while the equilibrium $u^* = 1$ is (locally) asymptotically stable for all $\tau < \frac{\pi}{2}$ and is unstable for $\tau > \frac{\pi}{2}$. At $\tau = \frac{\pi}{2}$ a Hopf bifurcation occurs with the birth of a periodic solution of eq. (2.13).

Actually, the global asymptotic stability of $u^* = 1$ has also been proved for all τ almost (but not exactly) up to $\frac{\pi}{2}$. Furthermore, in principle, the periodic solution arisen at $\tau = \frac{\pi}{2}$ may become unstable at some other value of τ through further bifurcations, but, as far as we know, numerical evidence shows that, for $\tau > \frac{\pi}{2}$ almost all solutions (those not starting at an equilibrium value, or at another periodic solution) are attracted to it. Moreover one can show that a Hopf bifurcation occurs also at $\tau = \frac{\pi}{2} + 2n\pi$ for each $n \geq 1$, giving rise to other periodic solutions that are however unstable.

We conclude this section by mentioning that model (2.2) can be analyzed along similar lines, finding (under appropriate conditions) a positive equilibrium N^* . Concerning stability of this equilibrium, after linearizing, we are led to the analysis of the characteristic equation

$$\lambda + a = be^{-\tau\lambda} \quad (2.16)$$

where

$$a = \mu, \quad b = e^{-\mu\tau} \rho'(N^*).$$

The details of the derivation are left as problems.

Equation (2.16) with parameters a and b includes both (2.9) and (2.15) as particular cases. Comparing this equation to (2.9), we see that b may be negative, if the function ρ satisfies the properties ascribed to scramble competition; in this case the analysis of (2.16) is rather different from (2.9) and may lead to conclusions similar to those obtained for the case of eq. (2.3). Problem 2.3 presents the steps of this analysis.

2.4 Distributed delay logistic model

Concerning eq. (2.4), it can be analyzed using similar techniques to those used for the equations with concentrated delay. However, with special kernels such as (2.5), eq. (2.4) can be transformed into a system of ODE. We focus on eq. (2.4) in the critical case of $\gamma = 0$ and leave the case $\gamma > 0$ as Problem 2.4.

In this case too we reduce to a dimensionless equations by the transformation

$$t \rightarrow \tilde{t} = rt, \quad N \rightarrow u = \eta N, \quad \tau \rightarrow \tilde{\tau} = r\tau,$$

in order to get

$$u'(t) = \left(1 - \int_{-\infty}^t K_i(t-s)u(s) ds\right) u(t), \quad (2.17)$$

where the kernels $K_i(t)$ have still the form (2.5) (with τ replaced by $\tilde{\tau}$).

Consider first the kernel $K_1(t)$ and define the auxiliary variable

$$Q(t) = \int_{-\infty}^t K_1(t-s)u(s) ds = \frac{1}{\tau} \int_{-\infty}^t e^{-\frac{t-s}{\tau}} u(s) ds,$$

where for $s \in (-\infty, 0)$ we use the initial heredity ϕ assigned in condition (2.7) so that $Q(0)$ is known. By direct derivation we have

$$Q'(t) = \frac{1}{\tau}u(t) - \frac{1}{\tau}Q(t),$$

and (2.4) transforms into the system

$$\begin{cases} u'(t) = (1 - Q(t))u(t), & u(0) = \phi(0) \\ Q'(t) = \frac{1}{\tau}u(t) - \frac{1}{\tau}Q(t), & Q(0) = \frac{1}{\tau} \int_{-\infty}^0 e^{\frac{s}{\tau}} \phi(s) ds. \end{cases} \quad (2.18)$$

Now (2.18) has the two equilibrium points (see Fig. 2.4)

$$E_0 = (0, 0), \quad E^* = (1, 1).$$

We study their stability by looking at the eigenvalues of the Jacobian matrix at each of them (see Appendix A)

Concerning E_0 the Jacobian matrix is

$$J(E_0) = \begin{pmatrix} 1 & 0 \\ \frac{1}{\tau} & -\frac{1}{\tau} \end{pmatrix},$$

with eigenvalues $\lambda_1 = 1$ and $\lambda_2 = -1/\tau$. Thus E_0 is a saddle point (unstable). The equilibrium E^* is instead stable since

$$J(E^*) = \begin{pmatrix} 0 & -1 \\ \frac{1}{\tau} & -\frac{1}{\tau} \end{pmatrix},$$

and

$$\text{Trace}(J(E^*)) = -\frac{1}{\tau} < 0, \quad \det(J(E^*)) = \frac{1}{\tau} > 0.$$

To go further and prove that actually E^* is a global attractor, we have to resort to the theory of planar systems (see Appendix A). Indeed, first we can exclude existence of periodic solutions by the Dulac function $L(u, Q) = \frac{1}{uQ}$ because

$$\text{Div} \left(\frac{1}{Q} - 1; \frac{1}{\tau Q} - \frac{1}{\tau u} \right) = -\frac{1}{\tau Q^2} < 0.$$

Then, we prove boundedness showing that in the phase plane of system (2.18), any region such as the one pictured in Fig. 2.4 is invariant for any $q > 1$ (a suitable choice of q allows to include any initial datum in such a region). This can be seen checking the vector field of the system on the boundary of the region. In fact, in Fig. 2.4 it is easy to check the field on the segments BC , CD , OD and OA , so we are left with AB . Now since AB lies on the line $u = \tau Q + q$, an outer normal has components $(1, -\tau)$

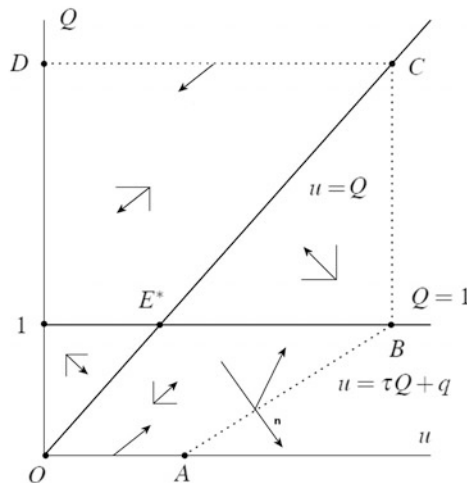


Fig. 2.4 Phase plane for the two-dimensional system (2.18). The segment AB lies on the line $u = \tau Q + q$ and the region $OABCD$ is invariant for any $q > 1$

and its scalar product with the differential field is

$$-\tau \left(\frac{1}{\tau} u(t) - \frac{1}{\tau} Q(t) \right) + (1 - Q)u = (1 - u)Q < 0$$

since $u \geq q > 1$ on AB . Boundedness of trajectories allows to apply Poincaré-Bendixon theorem and infer that the ω -limit set of any trajectory is not empty and, since there are no periodic solutions, contains only E^* . Thus, going back to eq. (2.17) we have:

for eq. (2.17), with the kernel $K_1(t)$, we have

$$\lim_{t \rightarrow +\infty} u(t) = 1$$

for any initial heredity $\phi(t)$, $t \in (-\infty, 0]$.

We conclude that model (2.4), with the fading memory kernel $K_1(t)$, though a more refined version of a logistic model, does ultimately present a similar behavior.

In the particular case of the kernel $K_2(t)$ of (2.5), we define

$$Q(t) = \frac{1}{\tau^2} \int_{-\infty}^t (t-s) e^{-\frac{t-s}{\tau}} u(s) ds, \quad W(t) = \frac{1}{\tau} \int_{-\infty}^t e^{-\frac{t-s}{\tau}} u(s) ds,$$

and we get the three-dimensional system

$$\begin{cases} u'(t) = (1 - Q(t))u(t), & u(0) = u_0, \\ Q'(t) = -\frac{1}{\tau}Q(t) + \frac{1}{\tau}W(t), & Q(0) = -\frac{1}{\tau^2} \int_{-\infty}^0 s e^{\frac{s}{\tau}} \phi(s) ds, \\ W'(t) = \frac{1}{\tau}u(t) - \frac{1}{\tau}W(t), & W(0) = \frac{1}{\tau} \int_{-\infty}^0 e^{\frac{s}{\tau}} \phi(s) ds. \end{cases}$$

Here we similarly have the steady states

$$E_0 = (0, 0, 0), \quad E^* = (1, 1, 1).$$

The Jacobian at E_0 is a block-triangular matrix and one can read the eigenvalues on its main diagonal (see Problem 2.4); one can then easily see that it is a saddle point. Concerning E^* we have the Jacobian

$$J(E^*) = \begin{pmatrix} 0 & -1 & 0 \\ 0 & -\frac{1}{\tau} & \frac{1}{\tau} \\ \frac{1}{\tau} & 0 & -\frac{1}{\tau} \end{pmatrix},$$

and its characteristic equation is

$$\tau^2 \lambda^3 + 2\tau \lambda^2 + \lambda + 1 = 0. \quad (2.19)$$

Applying the Routh-Hurwitz criterion (see Appendix A) we see that all the three roots of (2.19) have negative real part if

$$0 < \tau < 2;$$

hence, for $\tau < 2$, the equilibrium E^* is asymptotically stable. On the other hand, for $\tau > 2$, at least one root has positive real part so that E^* is unstable. Indeed, Equation (2.19) has two purely imaginary roots at $\tau = 2$, crossing the imaginary axis as τ increases so that conditions for a prelude to Hopf bifurcation are satisfied.

We summarize the results of this section as:

using kernel $K_1(t)$, corresponding to a fast fading memory, the equilibrium point is always asymptotically stable, as in the standard logistic model;
kernel $K_2(t)$, peaking at $t = \tau$, is able to produce sustained oscillations if τ is large enough, like the model with concentrated delay.

We remark that the examples considered above, although rather special, represent two different structures of the memory mechanisms. We also note that reduction to a system of ODE can be obtained for any kernel in the form

$$K(t) = \sum_{i=0}^n c_i t^i e^{-\frac{t}{\tau_i}}.$$

In this case an adequate number of auxiliary variables must be introduced.

2.5 Age structure and the renewal equation

Another source of delays in the context of population modeling is the *age structure* of the population itself. Actually, age is a major factor of differentiation among living organisms; in the present context, it is relevant that vital parameters like fertility and mortality generally depend on age, though the dependence may be mediated by individual size (see [7] for ecological models where size and growth enter directly). This observation calls for abandoning the framework where populations are assumed intrinsically homogeneous. Indeed, the variable $N(t)$ denoting the total number of individuals will not be sufficient to describe the state of a population but we should rather consider its *age distribution* at time t :

$$n(a, t) \quad a \in [0, a_+), \quad t \geq 0, \quad (2.20)$$

where a_+ denotes the *maximum age* which may be assumed to be finite or potentially infinite.

The distribution $n(a, t)$ is actually a density (dimensions $[N \times t^{-1}]$) so that the integral

$$\int_{a_1}^{a_2} n(a, t) da$$

gives the number of individuals who, at time t , have their age in the interval $[a_1, a_2]$.

Concerning the dynamics, we consider in this section an idealized situation that, when age structure is disregarded, corresponds to Malthus model. Thus we consider a single population living *isolated*, in an *invariant habitat*, all of its individuals being perfectly equal but for their age. In accordance with this phenomenological setting, *fertility* and *mortality* are intrinsic parameters of the population and do not depend on time, nor on the population size: they are functions of age only.

Thus we introduce:

- $\beta(a)$: **age-specific fertility**, the mean number of newborns per unit time, borne by each individual whose age is in the infinitesimal age interval $[a, a + da]$, at time t ;
- $\mu(a)$: **age-specific mortality**, the death rate of individuals having age in $[a, a + da]$ at time t .

Both $\beta(a)$ and $\mu(a)$ are non-negative functions of age, with dimensions $[t^{-1}]$. They are related to two fundamental ingredients of the demographic description. In fact we respectively define:

- **total birth rate**

$$B(t) = \int_0^{a_+} \beta(a) n(a, t) da, \quad (2.21)$$

the total number of newborns in unit time;

- **survival probability**

$$\Pi(a) = e^{-\int_0^a \mu(\sigma) d\sigma}, \quad a \in [0, a_+], \quad (2.22)$$

the probability for a newborn to survive to age a .

We emphasize that the birth rate $B(t)$ has dimension $[N \times t^{-1}]$ and that the number of births in the interval $(t, t + \Delta t)$ is equal to $\int_t^{t+\Delta t} B(s) ds$. Moreover we note that, concerning the survival probability $\Pi(a)$ it must be $\Pi(a_+) = 0$, and that its expression directly descends from the meaning of $\mu(a)$. In fact, consider a cohort of N individuals born at time 0 and let $N(a)$ the number of those that have survived to

age (and time) a . By the definition of age-specific mortality

$$N(a + da) \approx N(a) - \mu(a)N(a)da$$

hence

$$N'(a) = -\mu(a)N(a)$$

from which (2.22) follows. Since those that are aged a at time t must have been born at time $t - a$, the following relation, involving the survival probabilities, must clearly hold

$$n(a, t) = \Pi(a) B(t - a), \quad t \geq 0, \quad a \in [0, a_+]. \quad (2.23)$$

This shows that the birth rate $B(t)$ is a key variable from which the age distribution of the population can be derived. We note that to use (2.23) the birth rate $B(t)$ must be known for all $t > -a_+$. Thus, in order to have a well-defined mathematical problem, we assign the birth rate as an initial heredity

$$B(t) = \phi(t), \quad t \in [-a_+, 0]$$

corresponding to an initial age distribution assigned at $t = 0$

$$n(a, 0) = \Pi(a)\phi(-a), \quad a \in [0, a_+].$$

Now formula (2.23), together with (2.21), allows us to get an equation for the birth rate $B(t)$ connecting the two processes of births and deaths. In fact, substituting (2.23) into (2.21) we have,

$$B(t) = \int_0^{a_+} \beta(a)\Pi(a)B(t-a)da, \quad t \geq 0. \quad (2.24)$$

Cumulative variables

*Though the age distribution $n(a, t)$ contains all informations about the population state, other variables combining $n(a, t)$ with age-specific parameters and rates may be significant. The main cumulative variable is of course the birth rate $B(t)$ already considered in correspondence to the age-specific fertility, but we may consider other important examples such as the **total death rate***

$$D(t) = \int_0^{a_+} \mu(a)n(a, t)da, \quad (2.25)$$

*which, in the same spirit, gives the total number of deaths per unit time. The **total population** at time t ,*

$$N(t) = \int_0^{a_+} n(a, t)da, \quad (2.26)$$

may be considered if we are interested in some features that are not depending on the age of the individuals, as well as the size of other significant groups like **juveniles and adults**,

$$J(t) = \int_0^{a^*} n(a, t) da, \quad A(t) = \int_{a^*}^{a_{\dagger}} n(a, t) da, \quad (2.27)$$

where a^* denotes a “maturation” age. More generally, we may be interested in weighted selections such as

$$S(t) = \int_0^{a_{\dagger}} \gamma(a) n(a, t) da. \quad (2.28)$$

All these cumulative variables are important for models design and development.

From the mathematical point of view, (2.24) is a Volterra integral equation of the second kind because

$$B(t) = F(t) + \int_0^t K(t-s)B(s)ds, \quad (2.29)$$

with

$$K(t) = \beta(t)\Pi(t),$$

and

$$\begin{aligned} F(t) &= \int_t^\infty \beta(a)\Pi(a)\phi(t-a)da = \\ &= \int_{-\infty}^0 \beta(t-a)\Pi(t-a)\phi(a)da, \end{aligned}$$

where $t \geq 0$, and the functions β , Π , ϕ are extended by zero outside their definition intervals.

Equation (2.29) is known as the *renewal equation* and also as the *Lotka equation*. The convolution kernel $K(t)$ is called the *maternity function*. By (2.23), the solution and the analysis of this equation yields the dynamics of the age distribution of the population.

By a standard iterative procedure it is possible to prove existence of a non-negative solution of (2.29) (see problem 2.4). The asymptotic behavior of this solution, similarly to (2.1) is based on its asymptotic expansion over the set of exponential solutions of the equation. Namely, if we plug $B(t) = e^{\lambda t}$ into (2.24), we get the following characteristic equation for λ

$$1 = \int_0^\infty K(a)e^{-\lambda a} da. \quad (2.30)$$

This is called *Lotka characteristic equation*, where the right hand side is the Laplace transform of the kernel $K(t)$. For this equation it is possible to obtain a result similar to that obtained for eq. (2.9). Namely we have:

eq. (2.30) has one unique real solution $\lambda_0 = \alpha^*$. Any other solution λ_i is such that $\Re \lambda_i < \alpha^*$ and in each strip $\{\lambda \in \mathbb{C} | \Re \lambda \in [a, b]\}$ there is a finite number of roots.

This property yields the following formula for the birth rate

$$B(t) = b_0 e^{\alpha^* t} (1 + \Omega(t)), \quad (2.31)$$

with

$$\lim_{t \rightarrow +\infty} \Omega(t) = 0,$$

showing that asymptotically the population grows exponentially with trend α^* .

Similarly to (2.11), one may extend the asymptotic expansion to include the next roots with larger real part of (2.30) (occurring in complex conjugate pairs) to obtain sub-dominant exponential terms with an oscillatory component.

We note that, if the vital rates are independent of age (and $a_{\dagger} = +\infty$), (2.30) becomes

$$1 = \beta \int_0^{\infty} e^{-(\lambda + \mu)a} da = \frac{\beta}{\lambda + \mu}$$

so that

$$\alpha^* = \beta - \mu,$$

i.e. we have the usual Malthusian growth rate.

Going back to the age distribution $n(a, t)$, we use (2.31) in (2.23) getting

$$n(a, t) = b_0 e^{\alpha^*(t-a)} \Pi(a) (1 + \Omega(t-a)). \quad (2.32)$$

Thus $n(a, t)$ is asymptotic to the particular solution

$$n^*(a, t) = b_0 e^{\alpha^*(t-a)} \Pi(a). \quad (2.33)$$

This is called a *persistent solution* because the *age profile*

$$\omega(a, t) = \frac{n(a, t)}{N(t)},$$

calculated for (2.33) is actually constant

$$\omega^*(a) = \frac{e^{-\alpha^* a} \Pi(a)}{\int_0^{a_{\dagger}} e^{-\alpha^* a} \Pi(a) da}, \quad (2.34)$$

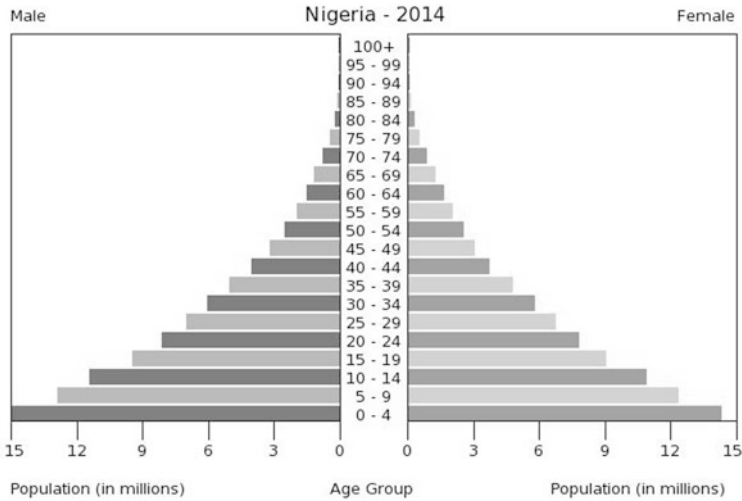


Fig. 2.5 The age pyramid (females and males are plotted separately) for the Nigerian population in the year 2014. The age pyramid can be related to the stable age distribution and its shape connected to the demographic parameters. Different types of profiles are due to different combinations of fertility and mortality. This picture can be compared with the one in Fig. 2.6. Source: USA Census Bureau, <http://www.census.gov>

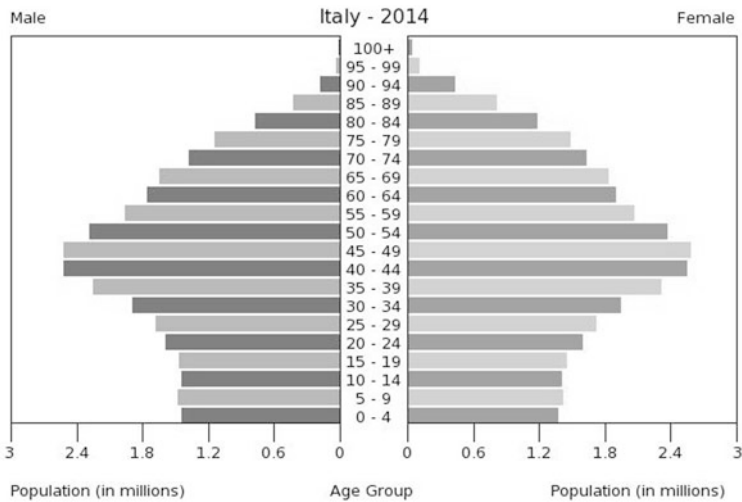


Fig. 2.6 The age pyramid of the Italian population in the year 2014. A different combination of fertility and mortality makes this picture different from that of Fig. 2.5. Source: USA Census Bureau, <http://www.census.gov>

and is called the *stable population profile* (see Figs. 2.5 and 2.6). The asymptotic result stated by (2.32) can be expressed as the so-called *stable population theorem*

that is a basic principle in demographic analysis:

starting with any initial distribution $n_0(a)$, the population eventually forgets its initial age distribution to attain the stable asymptotic profile $\omega^*(a)$ given by (2.34).

We may note that if α^* is positive then $\omega^*(a)$ is a decreasing function of age; if instead $\alpha^* < 0$ then $\omega^*(a)$ may be non decreasing. This fact may account for differences occurring in the shape of age pyramids of different populations (see Fig. 2.5 and Fig. 2.6), beyond the effects due to changes in demographic rates.

The basic reproduction number in the context of age structure

Given the relevance of α^ in determining the asymptotic behavior of solutions, finding ways to determining its value is very useful. An important property is that the sign of α^* (which determines growth or decline of the population) can be determined through the value of the basic parameter*

$$R_0 = \int_0^{a_1} \beta(a)\Pi(a) da. \quad (2.35)$$

Expression (2.35) for R_0 again corresponds to the number of newborn an individual is expected to produce during its life.

Indeed (see Problem 2.5) it can then be easily seen that

$$\alpha^* < 0 \quad (\text{resp. } > 0) \iff R_0 < 1 \quad (\text{resp. } > 1). \quad (2.36)$$

The population will then grow or decline, according to whether R_0 is greater or lower than 1.

2.6 Analysis of characteristic equations

The characteristic eqs. (2.9), (2.15) and (2.30) encountered in the analysis of stability are typical *transcendental* equations. Some general consideration about such equations are presented in Appendix B. Here we give some details about the results used in the previous sections.

First we consider (2.9) for which we have the basic result:

eq. (2.9) has one and only one real root α^* . Moreover, any other root is such that

$$\Re \lambda_i < \alpha^*$$

and, in each strip $\{\lambda \in \mathbb{C} \mid \Re \lambda \in [a, b]\}$, there is a finite number of roots at most.

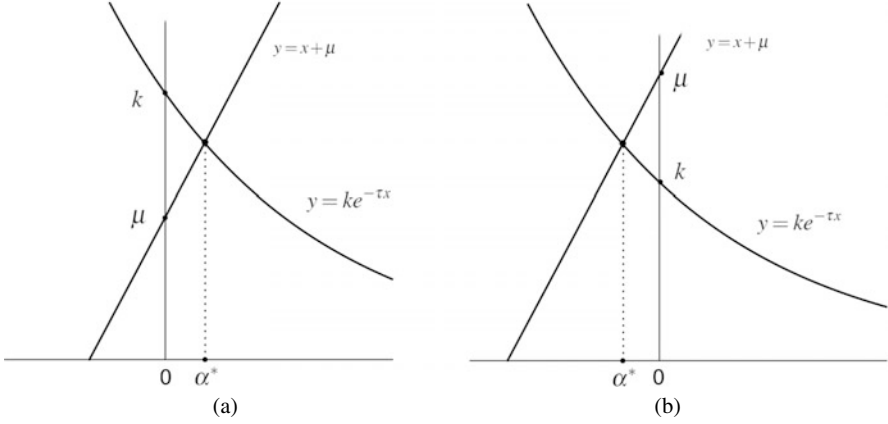


Fig. 2.7 The real root α^* of (2.9): (a) the case $k > \mu$ implying $\alpha^* > 0$; (b) the case $k < \mu$ implying $\alpha^* < 0$. The difference between the two cases is related to $R_0(\tau)$ defined in (2.12)

In fact, for real λ we can draw graphs (see Fig. 2.7) of the two functions

$$f(x) = k e^{-\tau x} \quad g(x) = x + \mu$$

to check that they have one and only one intersection corresponding to the unique real root α^* of (2.9).

Now we show that all complex roots λ of (2.9) satisfy $\Re \lambda < \alpha^*$, where α^* is the unique real root. To prove this fact let $\tilde{\lambda} = x + iy$ be one of these roots so that (2.9) gives

$$\begin{cases} i) & x + \mu = k e^{-\tau x} \cos(\tau y), \\ ii) & y = -k e^{-\tau x} \sin(\tau y). \end{cases}$$

Notice that if $x \geq \alpha^*$

$$x + \mu \geq \alpha^* + \mu = k e^{-\tau \alpha^*} \geq k e^{-\tau x} \geq k e^{-\tau x} \cos(\tau y).$$

If $x > \alpha^*$, the first inequality is strict so that $i)$ is impossible. On the other hand, if $x = \alpha^*$, all inequalities must be equalities, hence

$$\cos(\tau y) = 1$$

so that

$$\tau y = 2n\pi, \quad n = 0, 1, \dots$$

But then from $ii)$ we have

$$2n\pi = -\tau k e^{-\tau x} \sin(2n\pi) = 0.$$

Thus only $n = 0$ is allowed, i.e. $\tilde{\lambda} = \alpha^*$.

Finally, we show that in each strip $\{\lambda \in \mathbb{C} \mid \Re \lambda \in [a, b]\}$, there is a finite (possibly zero) number of roots. Indeed, we note that, if a root λ_i belongs to such a strip,

then

$$|\Im \lambda_i| = ke^{-\tau \Re \lambda_i} |\sin(\tau \Im \lambda_i)| \leq ke^{-\tau a}.$$

This means that all roots in the strip must belong to a bounded rectangle; on the other hand, it is known that a holomorphic function can have only a finite number of roots in a bounded set. The previous result allows to prove (2.10). We note that, by quite a similar argument, the same result can be proved for the characteristic eq. (2.30).

We now turn the attention to (2.15), first showing that, for τ small enough, all roots λ satisfy $\Re \lambda < 0$ (see Sect. 2.3). Indeed, setting $\lambda = x + iy$, (2.15) is transformed into the system

$$\begin{cases} x = -e^{-\tau x} \cos(\tau y) \\ y = e^{-\tau x} \sin(\tau y). \end{cases} \quad (2.37)$$

Then, if $\bar{\lambda} = \bar{x} + i\bar{y}$ is a root of (2.15) and $\bar{x} \geq 0$, by the second of (2.37) we must have

$$|\bar{y}| \leq e^{-\tau \bar{x}} \leq 1;$$

thus, if τ is sufficiently small (precisely $\tau < \frac{\pi}{2}$), we have

$$\cos(\tau \bar{y}) > 0$$

and, by the first of (2.37)

$$\bar{x} = -e^{-\tau \bar{x}} \cos(\tau \bar{y}) < 0,$$

which is a contradiction.

Furthermore, following the argument described in Sect. 2.3 about the path of roots as τ varies, we look for imaginary roots of (2.15) in order to determine whether crossings of the axis $\Re \lambda = 0$ occur and, if so, at which values of τ (see Fig. 2.3). Namely we look for solution in the form $\bar{\lambda} = i\bar{y}$, i.e. for solutions of

$$\begin{cases} 0 = \cos(\tau \bar{y}) \\ \bar{y} = \sin(\tau \bar{y}). \end{cases} \quad (2.38)$$

We consider only positive values of y , since we know that roots of (2.15) occur in conjugate pairs (if $x + iy$ solves (2.15), also $x - iy$ solves it), and it is clear from (2.15) that there are no nonnegative real roots.

The first of (2.38) yields

$$\tau \bar{y} = \frac{\pi}{2} + n\pi, \quad n = 0, 1, 2, \dots$$

which, plugged into the second equation, implies

$$\bar{y} = \sin\left(\frac{\pi}{2} + n\pi\right) = 1, \text{ and } n = 2k, \quad k = 0, 1, 2, \dots,$$

because we look for positive \bar{y} .

In conclusion, imaginary roots of (2.15) occur at the following values of τ

$$\tau_k = \frac{\pi}{2} + 2k\pi, \quad k = 0, 1, 2.$$

In particular, the first of these values is $\tau_0 = \frac{\pi}{2}$ corresponding to the two imaginary conjugate roots $\lambda_{\pm} = \pm i$.

We still have to check that these roots actually cross the imaginary axis to the right, namely we have to check that for the branch $\lambda(\tau) = x(\tau) + i y(\tau)$ we have $x'(\tau_0) > 0$. Now, from (2.15) we have

$$\left(1 - \tau e^{-\tau\lambda(\tau)}\right) \frac{d}{d\tau} \lambda(\tau) = \lambda(\tau) e^{-\tau\lambda(\tau)}.$$

Using $\tau = \tau_0$ and $\lambda(\tau_0) = i$, with some algebra one obtains

$$\frac{d\lambda}{d\tau} \Big|_{\tau=\tau_0} = \frac{1}{1 + \frac{\pi^2}{4}} \left(1 - i\frac{\pi}{2}\right),$$

i.e. $x'(\tau_0) > 0$. Thus for $\tau > \tau_0$ (and close enough to τ_0) $u^* = 1$ becomes unstable and the conditions for a prelude to Hopf bifurcation occur; hence we expect that a periodic solution arises.

The transcendental equations we have studied in this chapter are typical equations arising in the study of stability and generalize the polynomial characteristic equations of the O.D.E. case.

Problems

2.1. Delayed Malthus model

In model (2.1) of Sect. 2.2 we do not distinguish between pregnant and non-pregnant individuals, implying that a pregnant individual may be fertilized again during pregnancy. Since this may appear unlikely, we may wish to modify the model distinguishing between pregnant and non-pregnant individuals, and letting ϕ_0 the rate at which a non-pregnant individual becomes pregnant. Consider $N(t)$ as the sub-population of non-pregnant individuals, then:

1. Write a differential equation for the variable $N(t)$ considering as input the new-borns plus the individuals ceasing to be pregnant, and as output the individuals becoming pregnant plus those who die.
2. Check how the resulting model compares to model (2.1).

2.2. The method of steps

Using the method of steps outlined in Appendix C:

1. Consider the Malthus model (2.1) with

$$\tau = 1, \quad k = 3, \quad \mu = 1, \quad \phi(t) = 1 \quad \text{for } t \in [-1, 0],$$

and compute explicitly the solution of the model for $t \in [0, 2]$.

2. Compare the result with the corresponding Malthus model ($\tau = 0$).
3. Compute explicitly the solution of the logistic model (2.13) for $t \in [0, 1]$, with $\tau = 1$ and $\phi(t) = 0.8(1+t)$ for $t \in [-1, 0]$.
4. Find $t^* \in (0, 1]$ such that the previous solution satisfies $u(t^*) = 1$ so that its graph intersect the solution $u(t) \equiv 1$; explain why this fact does not contradict uniqueness.
5. Give a correct statement of well-posedness for delay models.

2.3. Non-linear models with gestation

Provide a specific form of model (2.2) choosing the functions $\rho(x)$ and $\mu(x)$ as in (1.28) and (1.29) (contest competition and scramble competition respectively) and scale the equations to obtain a dimensionless version. Then:

1. Find equilibria of the model in the two cases, discussing their existence as the parameters vary and comparing the results in the two cases.
2. Linearize the equations at each steady state to obtain the specific characteristic equations (2.16).
3. Discuss stability of the steady states through the analysis of the characteristic equations.

2.4. Distributed delay logistic model

Consider the general model (2.4), with $\gamma > 0$, endowed with one of the kernels (2.5), and scale the equation to obtain

$$u'(t) = \left(1 - \delta u(t) - \int_{-\infty}^t K(t-s)u(s)ds \right) u(t),$$

then:

1. Prove well-posedness through the sequence of iterates $\{u_n(t)\}$ defined as

$$u_n(t) = \phi(t), \quad \text{for } t \in (-\infty, 0];$$

and, for $t \in [0, +\infty)$,

$$\begin{aligned} u_0(t) &= \phi(0), \\ u_{n+1}(t) &= \phi(0) + \int_0^t \left(1 - u_n(\sigma) - \int_{-\infty}^{\sigma} K(t-s)u_n(s) ds \right) u_n(\sigma) d\sigma. \end{aligned}$$

2. Analyze existence and stability of steady states both for $K_1(t)$ and $K_2(t)$, reducing the problem to a system of ordinary differential equations (see Sect. 2.4).
3. Discuss if and how results differ from the previous analyzed cases.

2.5. The renewal equation

Consider the *renewal eq.* (2.29) ($K(t) \geq 0, F(t) \geq 0$), then:

1. State existence of a non-negative solution by proving convergence of the iterates

$$B_0(t) = F(t), \quad B_{n+1}(t) = F(t) + \int_0^t K(s)B_n(t-s) ds.$$

2. Consider the Laplace transform $\hat{B}(\lambda)$ and check that all its singularities are the roots of eq. (2.30).
3. Check that exponential solutions $e^{\lambda_i t}$ of (2.29) correspond to the solution of the characteristic eq. (2.30).
4. Prove that (2.30) has one and only one real solution α^* and that (2.36) holds.

2.6. Age structure

An alternative way of modeling age structure within the framework of Malthusian growth is provided by the following PDE system usually known as *Lotka-Von Foester-McKendrick model*

$$\begin{cases} i) \quad \frac{\partial n}{\partial t}(a, t) + \frac{\partial n}{\partial a}(a, t) + \mu(a)n(a, t) = 0, \\ ii) \quad n(0, t) = B(t) = \int_0^{a_{\dagger}} \beta(\sigma)n(\sigma, t) d\sigma, \\ iii) \quad n(a, 0) = n_0(a), \end{cases} \quad (2.39)$$

where equation (i) describes the aging and death process and equation (ii) the birth process, while (iii) is the initial condition.

The first equation is a first order partial differential equation on $n(a, t)$ in the strip $\{a \in [0, a_{\dagger}], t \geq 0\}$ with the boundary conditions ((2.39), ii) and ((2.39), iii) on the half-line $\{a = 0, t > 0\}$ and on the segment $\{a \in [0, a_{\dagger}], t = 0\}$, respectively. Condition (2.39)-ii is a non local boundary condition that makes the problem related to the renewal eq. (2.29) on the birth rate $B(t)$. Actually system (2.39) is equivalent to (2.29). Prove this equivalence through the following steps:

1. Prove that, if $B(t)$ is a differentiable solution to (2.29) with $\phi = \frac{n_0(-t)}{\Pi(-t)}$, then formula (2.23) provides a solution to (2.39).
2. Integrate eq. (2.39)-i along the characteristic lines $a - t = \text{const}$ to obtain (2.23) (see Fig. 2.8). Namely consider the transformation

$$p(a, t) = \frac{n(a, t)}{\Pi(a)}$$

so that (2.39)-i becomes

$$\frac{\partial p}{\partial t}(a, t) + \frac{\partial p}{\partial a}(a, t) = 0,$$

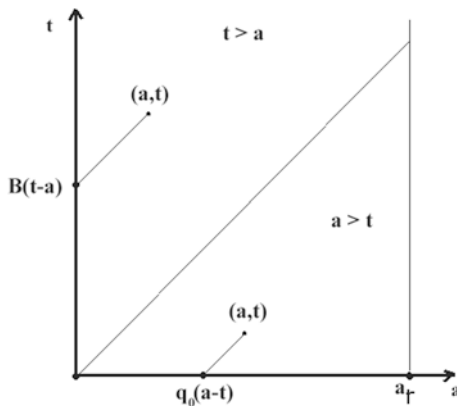


Fig. 2.8 Integration of eq. (2.39)-i along the characteristic lines $t - a = \text{const}$

with the general solution

$$p(a, t) = f(t - a)$$

where $f(\cdot)$ is any function. Then build the solution using (2.39)-ii and (2.39)-iii.

2.7. The stable population

Consider an age structured population growing according to the model discussed in Sect. 2.5. Suppose the population is in stable exponential growth, i.e. its distribution is given by (2.33) with a constant profile (2.34).

1. Give explicit formulae for the two quantities:

- A_m : the average age of the mothers of all children born at time t ;
- A_c : the average age at which the children born at time t will give birth during their life.

2. Show that

$$\text{if } \alpha^* > 0 \text{ then } A_m < A_c$$

(and vice versa if $\alpha^* < 0$).

3. Show that, when $R_0 \approx 1$, the following relation holds in first approximation

$$\alpha^* A_c \approx R_0 - 1.$$

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Models of discrete-time population growth

Ho l'impressione che non sia la prima volta che mi trovo in questa situazione: con l'arco appena allentato nella mano sinistra protesa avanti, la mano destra contratta all'indietro, la freccia F sospesa per aria a circa un terzo della sua traiettoria, e, un po' più in là, sospeso pure lui per aria e pure lui a circa un terzo della sua traiettoria, il leone L nell'atto di balzare su di me a fauci spalancate e artigli protesi Insomma il secondo t_0 in cui stanno la freccia F_0 e un po' più in là il leone L_0 e qui il me stesso Q_0 è uno strato spaziotemporale che resta fermo e identico per sempre, e accanto ad esso si dispone t_1 con la freccia F_1 e il leone L_1 e il me stesso Q_1 che hanno leggermente cambiato le loro posizioni, e lì affiancato c'è t_2 che contiene F_2 e L_2 e Q_2 e così via. In uno di questi secondi messi in fila risulta chiaro chi vive e chi muore tra il leone L_n e il me stesso Q_n , e nei secondi seguenti stanno certamente svolgendosi: o i festeggiamenti della tribù al cacciatore che ritorna con le spoglie del leone, o i funerali del cacciatore mentre attraverso la savana si diffonde il terrore al passaggio del leone assassino.¹

*Italo Calvino, "Ti con zero"
in "Ti con zero", 1967*

The models we have considered in the previous chapters are embedded in a continuous representation of the processes we study. Namely, both variables, time t and abundance $N(t)$, are real valued and are allowed to take any value. Use of continuous models lets us take advantage of the tools provided by calculus and, moreover, such a framework belongs to the traditional approach to modeling physical phenomena. However, since the 1970's, discrete time modeling has attracted more and more attention in population biology, because it seems to be natural in this context. In fact, population processes often occur through events concentrated in short time intervals

¹ I have the impression this isn't the first time I've found myself in this situation: with my bow just slackened in my outstretched left hand, my right hand drawn back, the arrow A suspended in midair at about a third of its trajectory, and, a bit farther on, also suspended in midair, and also at about a third of his trajectory, the lion L in the act of leaping upon me, jaws agape and daws extended. . . . In short, the second t_0 in which we have the arrow A_0 and a bit farther on the lion L_0 and here the me Q_0 is a space-time layer that remains motionless and identical forever, and next to it there is placed t_1 with the arrow A_1 and the lion L_1 and the me Q_1 who have slightly changed their positions, and beside that there is t_2 which contains A_2 and L_2 and Q_2 and so on. In one of these seconds placed in line it is clear who lives and who dies between the lion L_n and the me Q_n and in the following seconds there are surely taking place either the tribes's festivities for the hunter who returns with the lion's remains or the funeral of the hunter as through the savannah spreads the terror of the prowling murderous lion. (Translation by William Weaver)

(synchronized seasonal reproduction, egg deposition ...) and available data almost always consist in yearly (or obtained at other regular intervals) counts.

To build a discrete time framework we take a time interval Δt appropriate for the biology of the population under study; then, after enumerating the sequence of successive intervals with an integer index n , we denote by N_n the number of individuals at the beginning of the n -th interval. From the mathematical viewpoint we switch from differential equations to *difference equations* and we can rely on a somewhat parallel theory (see Appendix C). However the consequences we draw from these models often differ from those obtained from the analogous continuous models; this is especially true for one-dimensional systems, as the ones we have mainly examined so far. In this chapter we illustrate some features of discrete-time systems through a few classical examples that, though simple, have been used to discuss ecological systems. As ever, the analysis of the model tries to give an answer to the eternal dilemma of survival of the hunter or of the lion as well.

3.1 Discrete Malthus and Verhulst

We start with a discrete version of Malthus model based on the same assumptions introduced at the beginning of Sect. 1.2. However, instead of modeling the number of births and deaths in an arbitrary “short” time interval Δt , we use a fixed time step considered appropriate. For instance, the natural time step is 1 year for annual plants, univoltine insects, or most birds and mammals with a single reproductive season per year. When formulating a discrete-time model, it is useful to be precise about the time at which the intervals start; for instance, talking of annual plants we could define N_n as the number of seedlings at the beginning of the n -th growing season, or the number of mature plants at the end of the same season. In what follows, we will generally adhere to the second formulation, i.e. that counts are taken just before a reproduction event, though this does not change the model structure.

Thus we assume that every individual produces on average b new individuals in the following time-step (b accounts for the average number of offspring and for their probability to survive to the next reproductive season), and has probability s of surviving to next time-step.

We can then write the *difference equation*

$$N_{n+1} = bN_n + sN_n = mN_n \quad (3.1)$$

where $m = b + s$ is a dimensionless parameter, summarizing births and deaths.

If we wish to relate these parameters to Malthus model, discussed in Sect. 1.2, recall that the number of births in a “short” time interval Δt was assumed to be approximately $\beta \Delta t N_t$, thus we can define the fertility rate $\beta = b/\Delta t$. Similarly the number of deaths $\mu \Delta t N_t$ must be equal to those that do not survive $(1-s)N_t$, giving a mortality rate $\mu = (1-s)/\Delta t$. The case $\beta > \mu$ corresponds to $b + s > 1$, i.e. to $m > 1$, which is the condition for exponential growth, as can be easily seen from the expression below.

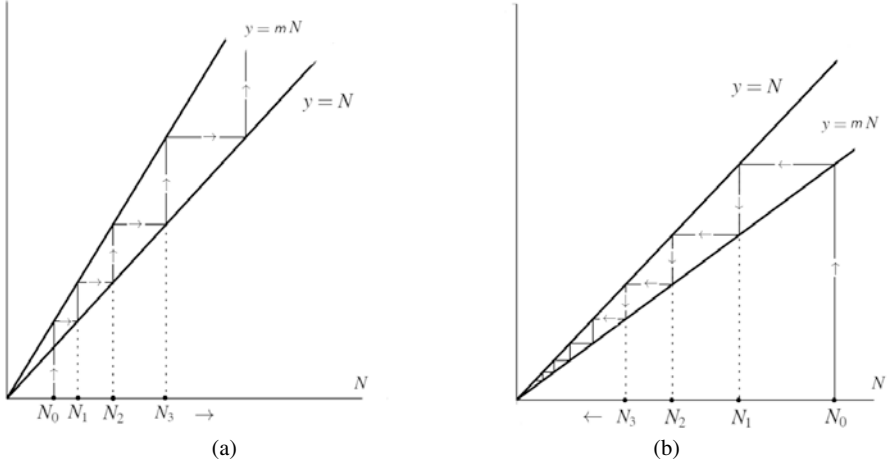


Fig. 3.1 Graphical construction (*cobwebbing method*) of the sequence for the discrete Malthus model (3.1), showing the results in (3.3): (a) the case of $m > 1$; (b) the case of $0 < m < 1$. The procedure is as follows: starting from N_0 on the x -axis, N_1 is the ordinate of the point (N_0, mN_0) reached with a vertical line from N_0 ; we find N_1 on the x -axis by drawing a horizontal segment from (N_0, mN_0) to the bisectrix. We have thus obtained N_1 from N_0 through the vertical segment to the line $y = mx$ and the horizontal segment to the line $y = x$; we can then obtain N_2 from N_1 with the same procedure, and continue onwards

Starting with N_0 initial individuals, by induction we have

$$N_n = m^n N_0. \quad (3.2)$$

Hence we conclude

$$\begin{aligned} m < 1 &\Rightarrow \lim_{n \rightarrow \infty} N_n = 0, \\ m > 1 &\Rightarrow \lim_{n \rightarrow \infty} N_n = +\infty, \\ m = 0 &\Rightarrow N_n = N_0. \end{aligned} \quad (3.3)$$

Namely we obtain the same conclusion as in the continuous Malthus model.

In Fig. 3.1 we show a well-known graphical procedure (the *cobwebbing method*) to build the iterates of a discrete model (the technique is explained in the legend to the figure). Both for $m > 1$ and $m < 1$, the procedure explains clearly the mechanism for exponential growth or decrease. This is quite pleonastic in this case, but it will be rather useful in all other cases.

In the same spirit as the discrete Malthus model, we now consider a discrete version of the logistic model, letting births b and survival s decrease linearly with population size as

$$b + s = m \left(1 - \frac{N}{K} \right)$$

where m and $K > 0$. Clearly it must be $N < K$ in order that $b + s > 0$.

In this case we have the difference equation

$$N_{n+1} = m \left(1 - \frac{N_n}{K} \right) N_n ,$$

that, scaled by defining the dimensionless variables

$$u_n = \frac{N_n}{K} ,$$

is transformed into

$$u_{n+1} = m(1 - u_n)u_n . \quad (3.4)$$

Equation (3.4) is a recursive formula to build the sequence u_n starting from a value u_0 . As mentioned above, we need $u_n \leq 1$ in order that u_{n+1} is positive. Hence we assign u_0 in $[0, 1]$ and require u_n in $[0, 1]$ for all n . Since $\max_{u \in [0,1]} mu(1-u) = \frac{m}{4}$, this is possible if and only if $m \leq 4$, which will be assumed from here onwards. It is not possible to obtain an explicit formula such as (3.2) for the solution, and the behavior of u_n has to be analyzed indirectly.

One possibility to gain some intuition about the behavior of the sequence $\{u_n\}$ is through the graphical cobwebbing procedure; two examples are shown in Fig. 3.2, one for $m \in (1, 2)$ that exhibits monotonic convergence to a fixed point; another one for $m \in (3, 3.4)$ where the sequences approaches a periodic solution of period 2. On the other hand, we can resort to the theory of discrete equations sketched in Appendix C. In fact, eq. (3.4) can be written as

$$u_{n+1} = F_m(u_n), \quad u_0 \text{ assigned}$$

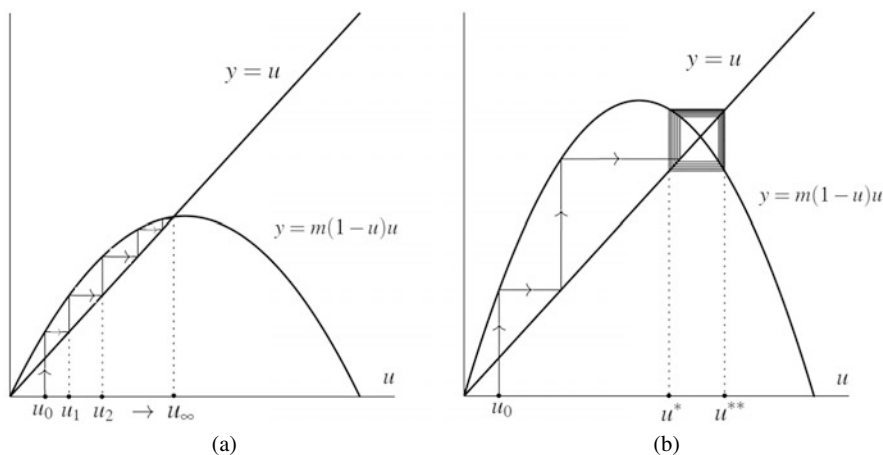


Fig. 3.2 The discrete logistic model (3.4) illustrated in two typical cases: (a) the case $1 < m < 2$, when the sequence u_n converges to the stationary solution $u_1^*(m)$; (b) the case $3 < m < 3.4$, when the stationary solution $u_1^*(m)$ is unstable and the solution tends to a periodic solution of period 2

with $F_m(x) = m(1-x)x$, emphasizing the dependence on the parameter m . The equilibria of the model can be found as fixed points of F_m , i.e. solutions of the equation

$$x = F_m(x) = m(1-x)x.$$

Thus we have the stationary solutions

$$u_0^*(m) = 0 \quad ; \quad u_1^*(m) = \frac{m-1}{m}$$

where the non trivial one exists for $m > 1$.

As far as the stability of these solutions is concerned, since $F'_m(x) = m(1-2x)x$ we have

$$F'_m(u_0^*(m)) = m, \quad F'_m(u_1^*(m)) = 2 - m.$$

Thus we conclude:

- the trivial equilibrium $u_0^*(m)$ is stable for $0 < m < 1$, unstable for $m > 1$;
- the equilibrium $u_1^*(m)$ is stable for $1 < m < 3$, unstable for $m > 3$.

At $m = 1$, a transcritical bifurcation occurs, with exchange of stability among equilibria, as we have already encountered several times. At $m = 3$ we encounter another type of bifurcation, which is typical of discrete systems: a *flip* or *period-doubling* bifurcation; namely, as the equilibrium (i. a. a “periodic solution of period 1”) becomes unstable, a periodic solution of period 2 emerges, inheriting the stability of the equilibrium.

Another graphical procedure, illustrated in Fig. 3.3, allows us to better understand the occurrence of 2-periodic solutions defined by

$$u_n = \begin{cases} u_{2k} &= u^*, \\ u_{2k+1} &= u^{**}, \end{cases} \quad (k = 0, 1, \dots).$$

In fact, the sequence u_n generated by (3.4) is split into the even-indexed and the odd indexed subsequences, respectively converging to u^* and to u^{**} . We also see that such periodic solution is an attractor. In the case of Fig. 3.3-(a) we have only the equilibrium u_1^* , while in the case of Fig. 3.3-(b) we have the point P with coordinates (u^*, u^{**}) .

Recalling that (see Appendix C) u^* and u^{**} are fixed points of the function

$$G_m(x) = F_m(F_m(x))$$

we can easily compute u^* and u^{**} in our specific case of the logistic discrete model. In fact we have

$$G_m(x) = m^2 x(1-x)(1-mx+mx^2)$$

and, after some routine algebra (we already know that $x = 0$ and $\bar{x} = \frac{m-1}{m}$ are solutions), the equation $G_m(x) = x$ takes the form

$$x(x - \bar{x})(m^2 x^2 - m(1+m)x + 1 + m) = 0.$$

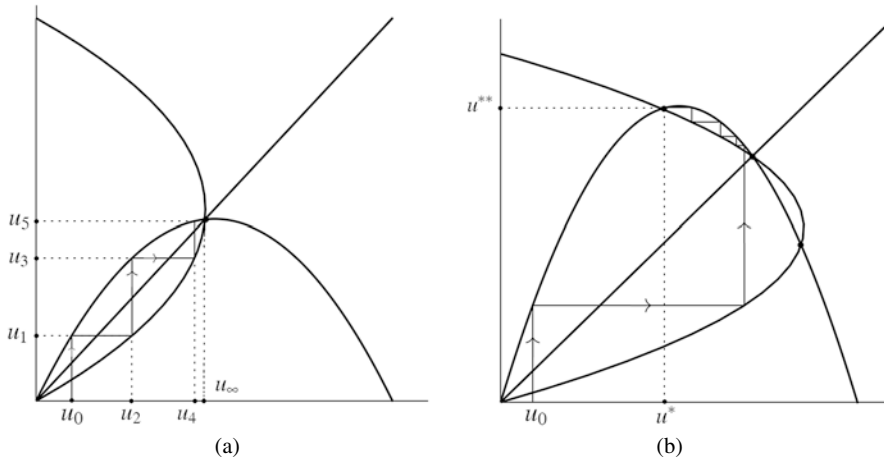


Fig. 3.3 Graphical procedure showing the even-indexed subsequence on the x -axis, and the odd-indexed subsequence on the y -axis; the two curves drawn are $y = F_m(x)$ and $x = F_m(y)$: from an even-indexed value like u_0 , the subsequent u_1 is found on the y -axis as the ordinate of $(u_0, F_m(u_0))$ found with a vertical line from u_0 to $y = F_m(x)$; then u_2 is the abscissa of the point $(F_m(u_1), u_1)$ found with a horizontal line from u_1 to the curve $x = F_m(y)$. (a) the case of a converging sequence ($m = 2$); (b) the case $m = 3.2$ when the even-indexed subsequence converges to u^* and the odd-indexed one converges to $u^{**} \neq u^*$

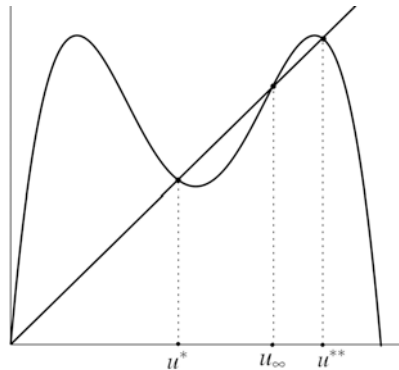


Fig. 3.4 The case $3 < m < m_4$ for the specific model (3.4): The function $G_m(x) = F_m(F_m(x))$ has three positive fixed points. The fixed point at u_∞ corresponds to the steady state (unstable), while u^* and u^{**} correspond to the periodic solution of period 2

Thus we have the two new fixed points

$$u^* = \frac{1+m-\sqrt{(m-1)^2-4}}{2m}, \quad u^{**} = \frac{1+m+\sqrt{(m-1)^2-4}}{2m},$$

occurring for $m > 3$, thus confirming that period-2 solutions exist only for m beyond the bifurcation point $m = 3$. In Fig. 3.4, we show the function $G_m(x)$ and its fixed points.

Performing a rigorous analysis beyond these preliminary conclusions requires more advanced tools, and we will not pursue it, while referring to more specialized texts (see [4, 7]). The main result concerning the global behavior of the sequence u_n is the following:

- if $m \leq 1$ the trivial equilibrium $u_0^*(m) = 0$ is a global attractor;
- if $1 < m < m_2 = 3$, the nontrivial equilibrium $u_1^*(m)$ is a global attractor;
- there exists an increasing sequence m_{2^k} ($m_2 = 3$) of bifurcation values (period-doubling bifurcation points) such that for $m_{2^k} < m < m_{2^{k+1}}$ there exists a globally attractive 2^k -periodic solution;
- the sequence m_{2^k} converges to $m^* \approx 3.57$; for $m > m^*$, the behavior is complex, generally of chaotic type (see the box below).

The previous results are summarized in the bifurcation graph of Fig. 3.5 and in Fig. 3.6 we show the outcome of the cobwebbing method in a case of chaotic solutions for $m > m^*$.

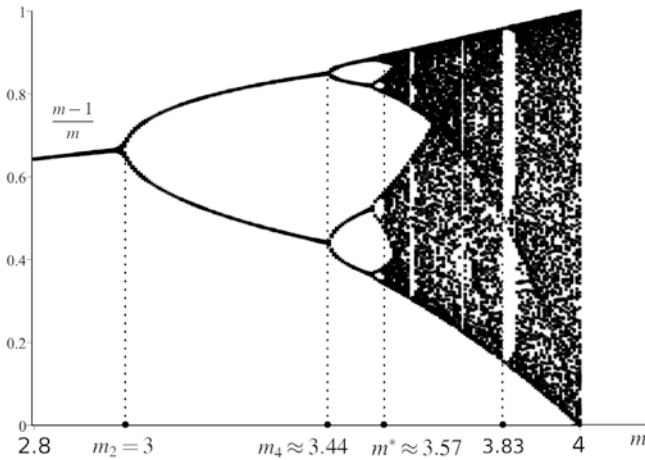


Fig. 3.5 Bifurcation graph of the discrete logistic equation for $m > 2.8$: for each value of m an initial value u_0 is chosen, and all points u_n for $150 < n \leq 300$ are plotted in correspondence to the abscissa m ; discarding the first 150 values aims at neglecting transient behavior and showing the attractor only. The figure illustrates the different cases of attractors: for $m \leq m_2 = 3$, the attractor is the point $(m-1)/m$; for $m_2 < m \leq m_4 \approx 3.44$, the attractor is the period-2 solution, giving rise, for $m > m_4$, to a 4-periodic solution; one can see also m_8 , where an attracting 8-periodic solution emerges, but the following period-doubling bifurcations cannot be seen, as they accumulate at $m^* \approx 3.57$. Beyond m^* , the solutions have generally a complex behavior, in most cases of chaotic type, though values of m with a more regular behavior exist: for instance for $m = 3.83$, almost all initial values u_0 are attracted to a unique 3-periodic solution

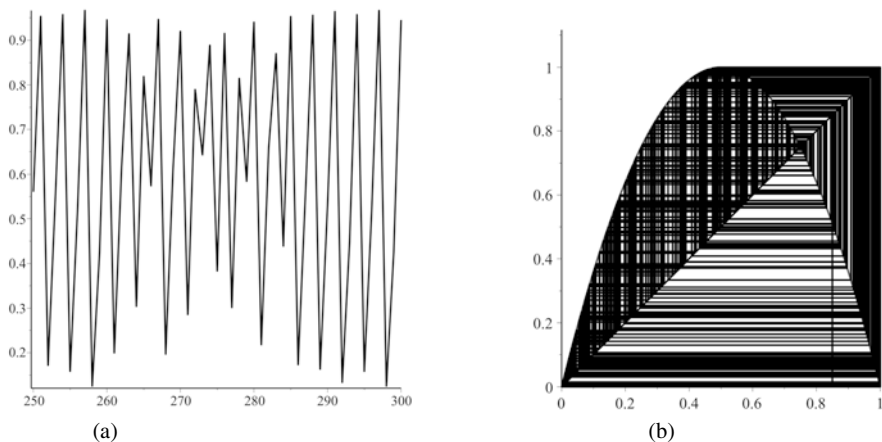


Fig. 3.6 Examples of chaotic behavior of the sequence u_n : (a) u_n vs. n for $m = 3.8$; (b) cobweb diagram for $m = 4$

The parameter value m^* represents a switching point above which the sequence u_n has no predictable behavior (chaotic, in fact), while for any value below m^* it is attracted by a periodic solution that, though very complex, is however well defined. Actually, for each value of $m < m^*$ there is a finite set of periodic solutions, all unstable but one, while for $m > m^*$ we have a sequence of unstable periodic solutions and any other solution wanders around.

Clearing chaos about chaos

The word **chaos** is an evocative one suggesting mythological views of the universe, concerning both its origin and its end. As far as we can say, the word ‘chaos’ was introduced in mathematics in correspondence of the discovery (and actually the rediscovery of older results, due to Poincaré at the end of XIX century, and to Lorenz and Sarkovskii in the 1960’s) that simple models like the discrete logistic could give rise to complex behaviors. The word chaos implied that deterministic models can yield outputs that resemble random noise, and seem as unpredictable as that.

Although a unique mathematical definition of **chaos** does not really exist, the one given by Devaney [4] seems to have been the most influential, at least in the mathematical context, since it can be (more or less easily) checked and appears to capture the essence of the phenomenon, an interplay between regularity and unpredictability. Devaney’s definition of chaos consists in 3 conditions. Skipping the more technical one (topological transitivity), the two others are:

- for any u_0 and for any $\delta > 0$ there exists a u'_0 with $|u_0 - u'_0| < \delta$ such that the sequence starting from u'_0 is periodic;

- *there exists a constant c such that for any u_0 and for any $\delta > 0$ there exists a u'_0 with $|u_0 - u'_0| < \delta$ and $n > 0$ such that $|u_n - u'_n| > c$.*

The second condition (sensitive dependence on initial data) states that, however slightly one changes the initial point, the new solution would be rather different from the first one. In this sense, even if we perfectly knew the laws of nature, still the long-term future would be unpredictable, given that initial values cannot be known with complete accuracy. In other words, the famous Brazilian butterfly, flapping its wings, could accidentally produce a tornado in Texas (see [6]).

On the other hand, the first condition ensures that solutions u_n appear similar to periodic, when looked over short periods of time (see Fig. 3.6). Thus, it is possible to perform short-term predictions of the system, differently from purely random variability. There actually techniques to estimate the degree (i.e., the time-horizon for a certain accuracy) of predictability of a chaotic system (see, for instance, [2]).

This mixture of short-term predictability and long-term unpredictability is the hallmark of what is now named 'chaos'. The logistic discrete model presented in Sect. 3.1 provides a very popular and paradigmatic example (also from the historical point of view), but chaotic behavior (with a simple extension of the definition) can appear also in non-linear systems in continuous time (as long as they consist of at least 3 ordinary differential equations) and indeed has been found, as we will see in later chapters, in several ecological models. This has been considered as a possible explanation of the complexity recorded in population data (see [8, 9]), in alternative or in addition to random perturbations in the habitat or in the species densities.

3.2 Other simple models

After seeing the models of the previous section, it can be understood that the general scheme for the discrete-time modeling of a homogeneous population is the recursive law

$$N_{n+1} = F(N_n), \quad N_0 \text{ assigned.} \quad (3.5)$$

where N_n denotes as usual the number of individuals in the n -th time interval and the function $F : [0, +\infty) \rightarrow [0, +\infty)$ describes the outcome of the birth and death process, through the time step Δt . Thus $F(x)$ is conveniently supposed to be non-negative (contrary to the case of the logistic map $F(x) = mx(1-x)$, used in the previous section, which is nonnegative only for $x \in [0, 1]$), and is usually represented through a *per capita net growth rate* $R(x)$ reflecting the mechanism of growth.

$$F(x) = R(x)x.$$

The non-linear logistic model examined in the previous section has a universally recognized historical role, but other models appear to be more adequate to represent the

mechanisms of population growth. Specifically, we consider here the Beverton-Holt and Ricker models, first used to model recruitment in fisheries, which exemplify the cases of contest and scramble competition introduced in Chap. 1, Sect. 1.5. In fact the two different mechanisms have suggested the following forms for $F(x)$ (see (1.28) and (1.29))

$$F(x) = \frac{\alpha x}{1 + vx} \quad (\text{Beverton-Holt model}) \quad (3.6)$$

$$F(x) = \alpha x e^{-vx} \quad (\text{Ricker model}) \quad (3.7)$$

where α and v are positive constants tuning the model. Both models can be rescaled taking $u_n = vN_n$, so that we respectively have the functions

$$F(x) = \frac{\alpha x}{1 + x}, \quad F(x) = \alpha e^{-x} x.$$

For both models there exists the extinction equilibrium $u_0^*(\alpha) = 0$, and a positive equilibrium, given respectively by

$$u_1^*(\alpha) = \alpha - 1 \quad (\text{Beverton-Holt}) \quad \text{and} \quad u_1^*(\alpha) = \ln \alpha \quad (\text{Ricker}).$$

The equilibria $u_1^*(\alpha)$ exist only for $\alpha > 1$, as shown in the bifurcation graphs of Fig. 3.7.

Concerning stability, in the case of the (scaled) Beverton-Holt model we have

$$F'(x) = \frac{\alpha}{(1+x)^2}, \quad F'(0) = \alpha, \quad F'(u_1^*(\alpha)) = \frac{1}{\alpha}$$

and we have the bifurcation diagram of Fig. 3.7-(a) showing supercritical bifurcation at $\alpha = 1$, with the positive equilibrium remaining asymptotically stable for all $\alpha > 1$.

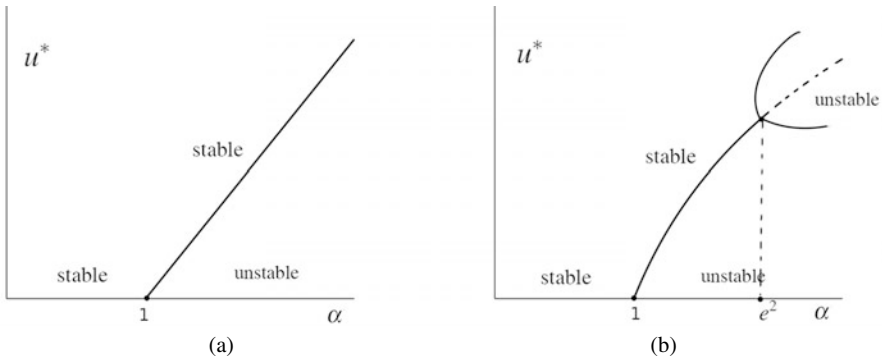


Fig. 3.7 Bifurcation diagrams for models (3.6) and (3.7): (a) the Beverton-Holt model, supercritical bifurcation at $\alpha = 1$ no doubling periods; (b) the Ricker model, supercritical bifurcation at $\alpha = 1$ and doubling period at $\alpha = e^2$

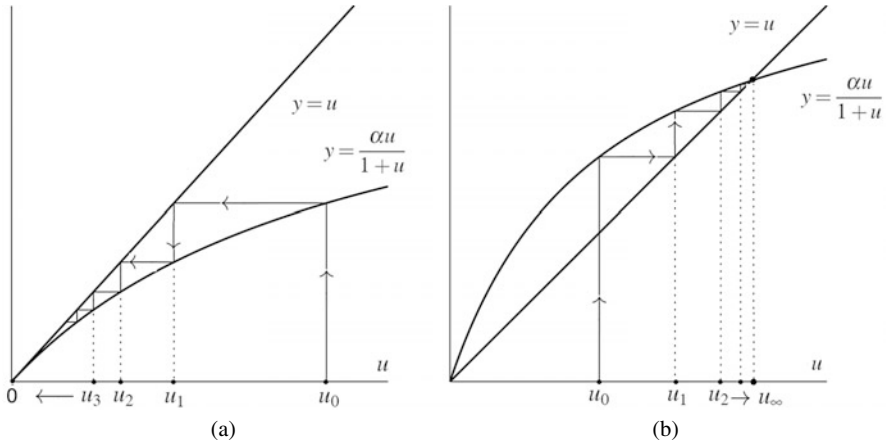


Fig. 3.8 The cobwebbing procedure for Beverton-Holt model. The sequence produced is monotonically converging to an equilibrium. (a) shows the case $\alpha < 1$ when the sequence converges to 0; (b) the case $\alpha > 1$ is shown when the sequence converges to the non-trivial equilibrium

As $F(x)$ is an increasing function, the cobwebbing procedure (see Fig. 3.8) suggests that:

if $\alpha \leq 1$, all solutions of Beverton-Holt model converge to the extinction equilibrium $u_0^*(\alpha) = 0$; if $\alpha > 1$ they all converge to $u_1^*(\alpha)$.

This statement can be easily proved, as asked in Problem 3.3. Thus Beverton-Holt model, related to contest competition, shows the behavior typical of continuous logistic models designed through differential equation. For this reason it is considered as the true discrete equivalent of the logistic model, more than the quadratic model of Sect. 3.1. Indeed, looking at the solutions of Verhulst logistic model at discrete time steps, one obtains Beverton-Holt model, as proposed in Problem 3.4.

Concerning Ricker model, an analogous computation shows that

$$F'(x) = \alpha(1-x)e^{-x}, \quad F'(0) = \alpha, \quad F'(u_1^*(\alpha)) = 1 - \ln \alpha.$$

Thus the extinction equilibrium $u_0^*(\alpha)$ is stable for $\alpha < 1$ while $u_1^*(\alpha)$ is stable for $\alpha \in (1, e^2)$. Analogously to what seen for the discrete logistic model, a periodic solution of period 2 appears through the presence of a flip bifurcation at $\alpha = e^2$ for $\alpha > e^2$ (see the bifurcation diagram in Fig. 3.7-(b)).

This can actually be proved by direct methods. In fact, since

$$G(x) = F(F(x)) = \alpha^2 x e^{-x(1+\alpha e^{-x})}$$

the equation $x = F(F(x))$ becomes, through simple algebraic steps,

$$x = \frac{2 \ln \alpha}{1 + \alpha e^{-x}} \quad (3.8)$$

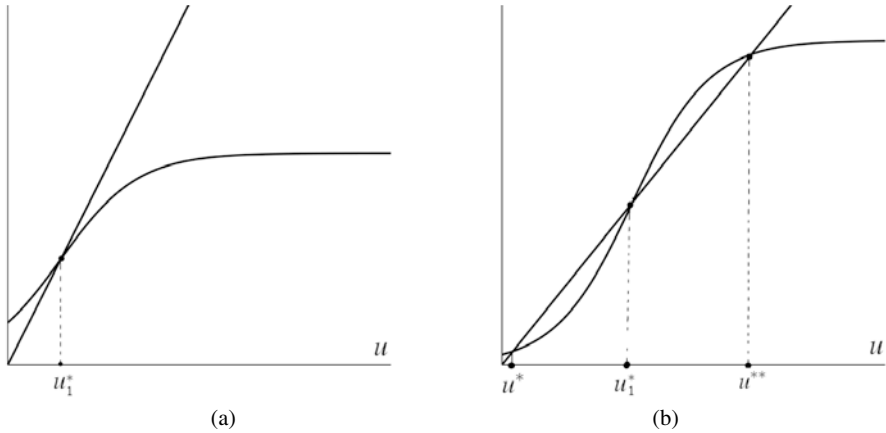


Fig. 3.9 Graphical solution of eq. (3.8) for $\alpha < e^2$ (a) and $\alpha > e^2$ (b): plots of the line $y = x$ and of the function $y = \frac{2 \ln \alpha}{1 + \alpha e^{-x}}$ in order to determine intersections

which has two solutions, different from $x = 0$ and $x = \ln \alpha$, if and only if $\ln \alpha > 2$ (see Fig. 3.9). Similarly to the logistic-quadratic model examined in the previous section, to this first period-doubling bifurcation point, a ‘cascade’ of further period-doubling bifurcations follows, with transition to chaos as in the case of the quadratic model. Thus we have:

if $\alpha \leq 1$, all solutions of Ricker model converge to the extinction equilibrium $u_0^*(\alpha) = 0$, if $1 < \alpha < e^2$ they all converge to $u_1^*(\alpha)$; at $\alpha = e^2$ a first period-doubling bifurcation occurs, followed by a sequence of further bifurcations leading to chaotic behavior.

A striking result that was obtained is that this period-doubling route to chaos is universal for unimodal maps [5]. Namely, given any sufficiently regular unimodal function $F(\cdot)$ defined on $[0, +\infty)$ such that $F(0) = 0 = \lim_{x \rightarrow \infty} F(x)$, if we consider the sequences $u_n = \alpha F(u_{n-1})$, there exists an increasing sequence α_{2^k} , $k \geq 0$, such that $\lim_{k \rightarrow \infty} \alpha_{2^k} = \alpha^*$, for $\alpha \in (\alpha_{2^k}, \alpha_{2^{k+1}})$ there exists a 2^k -periodic solution which is globally attractive, while for $\alpha > \alpha^*$ the sequences have a chaotic behavior. Further, the limit of $\frac{\alpha_{2^k} - \alpha_{2^{k-1}}}{\alpha_{2^{k+1}} - \alpha_{2^k}}$ exists, and is independent of the function $F(\cdot)$.

This last clause is very intriguing mathematically, but does not seem to give particular biological insights. Instead, the fact that any discrete population model with a humped recursion function (that, as discussed above, can derive from scramble competition) can give rise to chaotic behavior is a basic difference from continuous model for one species growth.

Discrete models and numerical schemes

A well known source of difference equations is the discretization of differential equations. In fact, numerical analysis has its focus on the design of efficient schemes to provide good approximations of solutions that on their side are continuous functions of the variables. In this perspective, the discrete Malthus model (3.1) can be viewed as a discretization of the differential eq. (1.3) (an explicit Euler scheme, in fact). However, the viewpoint motivating the discrete modeling approach is quite different because in this case the time interval Δt is considered an ingredient of the phenomena described by the model, while in the case of a numerical scheme it is intended as a necessary finite approximation of an infinitesimal step and, in principle, it must be taken as small as possible.

Once a numerical scheme for a continuous model has been derived, it can be worthwhile studying the behavior of the method, using techniques of the type illustrated in this chapter. Doing this may be important to check that the properties of the numerical scheme resemble those of the original continuous model, but has nothing to do with discrete-time population models, that should be derived on the basis of the biological features of the process.

3.3 Discrete dynamics involving age-classes

We move one step further in this modeling framework, by recognizing that a population can be split into *juveniles* and *adults*, with only adults reproducing. Furthermore, we assume that juveniles require exactly one time step to become adults.

The scheme of transitions is illustrated in Fig. 3.10, where:

- J_n = number of juveniles at the discrete time n ;
- A_n = number of adults at the discrete time n ;

and the total population is given by

$$N_n = J_n + A_n .$$

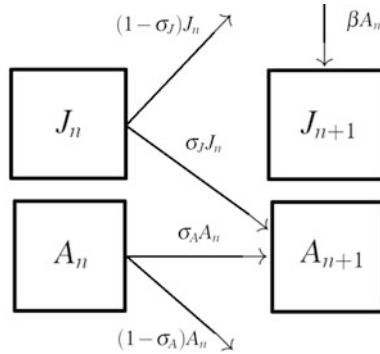


Fig. 3.10 A compartmental description of the dynamics of a population structured into the two classes of juveniles and adults. The resulting linear model (3.9) may be considered as the analogous of Malthus model

Introducing the parameters:

- β = per capita number of newborns;
- σ_J = survival probability of juveniles;
- σ_A = survival probability of adults;

we have the system of recursive equations

$$\begin{cases} J_{n+1} = \beta A_n \\ A_{n+1} = \sigma_J J_n + \sigma_A A_n \end{cases} \quad (3.9)$$

Defining $\mathbf{N}_n \equiv (J_n, A_n)$, system (3.9) can be put in the vector form

$$\mathbf{N}_{n+1} = \mathbf{A} \mathbf{N}_n \quad (3.10)$$

where the matrix \mathbf{A} is defined as

$$\mathbf{A} \equiv \begin{pmatrix} 0 & \beta \\ \sigma_J & \sigma_A \end{pmatrix}. \quad (3.11)$$

Then the solution is explicitly given by

$$\mathbf{N}_n = \mathbf{A}^n \mathbf{N}_0 \quad (3.12)$$

where \mathbf{N}_0 is assigned. Note that, since all entries of the matrix \mathbf{A} are non-negative, if \mathbf{N}_0 is non-negative (i.e. has non-negative components) then \mathbf{N}_n is also non-negative.

In order to determine the structure of the solution, we look for the eigenvalues λ_{\pm} of the matrix \mathbf{A} , with their respective eigenvectors \mathbf{V}_{\pm} . In fact we have (see Appendix C)

$$\mathbf{N}_n = c_+ \lambda_+^n \mathbf{V}_+ + c_- \lambda_-^n \mathbf{V}_-,$$

where the constants c_{\pm} are determined by

$$\mathbf{N}_0 = c_+ \mathbf{V}_+ + c_- \mathbf{V}_- .$$

To determine the asymptotic behavior of the solution, we need to check the condition

$$|\lambda_{\pm}| < 1 .$$

Now, we have

$$\lambda_{\pm} = \frac{1}{2} \left(\sigma_A \pm \sqrt{\sigma_A^2 + 4\beta\sigma_J} \right) ,$$

and, since $|\lambda_-| < |\lambda_+|$, we are left with λ_+ . Indeed, it is easy to check that:

$$|\lambda_+| < 1 \quad \text{if and only if} \quad \beta\sigma_J > 1 - \sigma_A . \quad (3.13)$$

This condition is related to the basic reproduction number R_0 , i.e. to the number of newborns that one individual produces in its whole life. In fact, in this case we have (compare with (1.6) for the Malthus model)

$$R_0 = \frac{\beta\sigma_J}{1 - \sigma_A} , \quad (3.14)$$

as we can check counting all newborns through the (infinite) time steps of the life of one individual (or of a cohort, considered of unit size, of individuals); namely

- *first step* (from $n = 0$ to $n = 1$): the individual still belongs to the juveniles class and no newborns are produced; however we have to consider the survival probability σ_J to count the probability that the individual is alive (or how much of that cohort is left) after the first step (when it becomes an adult);
- *second step* (from $n = 1$ to $n = 2$): the survived fraction of the initial cohort (now adults) produces β newborns so that we have to count $\beta\sigma_J$ newborns; moreover the cohort is further reduced to $\sigma_A\sigma_J$;
- *further steps* (from n to $n + 1$): going on ... after n steps the cohort is reduced to $\sigma_A^{n-1}\sigma_J$ and produces $\beta\sigma_A^{n-1}\sigma_J$ newborns; moreover it is reduced to $\sigma_A^n\sigma_J$.

In conclusion, to compute R_0 we have to sum all the newborns counted in each step

$$R_0 = \sum_{n=0}^{\infty} \beta\sigma_A^n\sigma_J = \frac{\beta\sigma_J}{1 - \sigma_A} ,$$

that is (3.14). Thus the previous statement (3.13) can be rephrased as:

if $R_0 < 1$ the population goes extinct; if instead $R_0 > 1$, the population survives and grows indefinitely.

Note that if $\beta = \sigma_J = \sigma_A = 1$, model (3.9) becomes

$$\begin{cases} J_{n+1} = A_n \\ A_{n+1} = J_n + A_n \end{cases} \quad (3.15)$$

Thus, substituting $J_n = A_{n-1}$ (the first equation) into the second equation, we have the difference equation

$$A_{n+1} = A_n + A_{n-1}$$

producing the well known Fibonacci sequence.

A general linear model, involving a certain number of age classes a_+ , generalizing (3.9), is given by the following system

$$\begin{cases} N_1^{n+1} = \sum_{i=1}^{i=a_+} \beta_i N_i^n \\ N_i^{n+1} = \sigma_{i-1} N_{i-1}^n, \quad i = 2, \dots, a_+ \end{cases} \quad (3.16)$$

where the state variable N_i^n denotes the number of individuals in the age class i at time n , and the parameters are defined as:

- β_i = fertility of an individual of age i ;
- σ_i = survival probability of individuals of age i .

Namely the first equation in (3.16) describes the reproduction process, counting the number of newborns from each age class of the previous time-step and including them in the age class $i = 1$; the other equations count how many individuals survive from one year to the next, moving from age class $i - 1$ to age class i . Note that, differently from the previous adult-juvenile model, it is assumed that individuals in the last age class cannot survive, so that N_{a_+} represents the number of individuals of exactly age a_+ ; if useful, this can be easily amended, without radical changes in what follows.

Models of this type are routinely used for many long-lived populations, including human ones. Generally only females are counted and the fertilities β_i are taken as the product of the actual births times the sex ratio at birth.

Equation (3.16) can be written in vector form, by letting

$$\mathbf{N}_n = (N_1^n \cdots N_{a_+}^n).$$

Then

$$\mathbf{N}_{n+1} = \mathbf{A} \mathbf{N}_n \quad (3.17)$$

where A is an $a_+ \times a_+$ matrix, called a *Leslie matrix*:

$$A \equiv \begin{pmatrix} \beta_1 & \beta_2 & \cdots & \beta_{a_+-1} & \beta_{a_+} \\ \sigma_1 & 0 & \cdots & 0 & 0 \\ 0 & \sigma_2 & \cdots & 0 & 0 \\ \cdot & \cdot & \cdots & \cdot & \cdot \\ 0 & 0 & \cdots & \sigma_{a_+-1} & 0 \end{pmatrix}. \quad (3.18)$$

Note the strict analogy of this discrete model with the model of Sect. 2.5; the analogy will also be seen in the results emerging from its analysis, that we will now perform under the assumptions:

- L1) $\sigma_1, \sigma_2, \dots, \sigma_{a_+-1} > 0$ (otherwise, nobody would survive to the final age class, and we could use fewer of them);
- L2) $\beta_{a_+} > 0$ (if the old age classes were not reproductive, we consider only age classes up to the last reproductive one. Problem 3.6 will show how it is possible to always reduce to this case);
- L3) $\beta_{a_+-1} > 0$ (this is a simple hypothesis sufficient to synchronize all age classes. Problem 3.7 will explore what can happen without that assumption).

Iterating (3.17), one arrives again at $\mathbf{N}_n = A^n \mathbf{N}_0$ and $A^n \mathbf{N}_0$ can be written in terms of the eigenvalues and eigenvectors of A . In particular, if there is a leading eigenvalue λ_0 , i.e. an eigenvalue such that

$$|\lambda_0| > |\lambda_j|, \quad \text{for any other eigenvalue } \lambda_j \text{ of } A,$$

then

$$\mathbf{N}_n = A^n \mathbf{N}_0 = \lambda_0^n (c_0 \mathbf{V}_0 + \omega_n) \quad (3.19)$$

where \mathbf{V}_0 is a (normalized) eigenvector of A corresponding to λ_0 , c_0 is the component relative to \mathbf{V}_0 of the initial vector \mathbf{N}_0 and ω_n is a sequence of vectors (reflecting the components of \mathbf{N}_0 in the other vectors of the spectral basis) such that $\lim_{n \rightarrow \infty} \omega_n = 0$.

Perron-Frobenius theory (see for instance [10]), and the previous assumptions, ensure the leading eigenvalue λ_0 exists and is real and positive. This result can also be seen directly, as asked in Problem 3.5, through several steps. The first step is noticing that, for any eigenvalue λ of A , necessarily the corresponding eigenvectors $\mathbf{V} \equiv (V_1, \dots, V_n)$ satisfy

$$V_i = \pi_i \lambda^{-(i-1)} V_1 \quad (3.20)$$

where

$$\pi_1 = 1, \quad \pi_i = \sigma_{i-1} \pi_{i-1} = \sigma_1 \cdots \sigma_{i-1}$$

is the probability of surviving up to age i .

Identity (3.20) follows immediately by equating recursively the rows from 2 to a_+ of the relation $A\mathbf{V} = \lambda\mathbf{V}$. One then finds that λ_0 is the unique positive root of

$$H(\lambda) := \sum_{i=1}^{a_+} \beta_i \pi_i \lambda^{-i} = 1. \quad (3.21)$$

As H is decreasing with λ on $(0, \infty)$, it is clear that $\lambda_0 > 1$ (resp. $= 1$ or < 1), if and only if $H(1) > 1$ (resp. $= 1$ or < 1). We can then introduce the reproduction number

$$R_0 = H(1) = \sum_{i=1}^{a_+} \beta_i \pi_i. \quad (3.22)$$

Indeed, for each age i , by multiplying the probability π_i of surviving to age i times the fertility β_i at that age, $\beta_i \pi_i$ represents the expected number of children borne at age i . Thus, by summing over all ages i , R_0 represents the expected number of children borne over all an individual's life.

Since from (3.20) the eigenvector corresponding to λ_0 reads

$$\mathbf{V}_0 \equiv \left(1, \dots, \pi_i \lambda_0^{-(i-1)}, \dots, \pi_{a_+} \lambda_0^{-(a_+-1)} \right),$$

then from (3.19) we have obtained:

for any initial vector \mathbf{N}_0 of the initial distribution of the population, for large n

$$N_i^n \approx c_0 \pi_i \lambda_0^{n-i} \quad (3.23)$$

where λ_0 is the only positive solution of (3.21), π_i is the probability of surviving to age i and c_0 is a positive constant depending on the initial vector \mathbf{N}_0 ; furthermore $\lambda_0 > 1$ (resp. $= 1$ or < 1) if and only if the reproduction number $R_0 > 1$ (resp. $= 1$ or < 1).

3.4 A non-linear model of adult-juvenile dynamics

The previous models can be extended by allowing for a dependence of parameters on population densities. For the sake of simplicity, we limit ourselves to consider the juvenile-adult model (3.9), and introduce a density-dependence in reproductive rate only. Namely, we replace the parameter β with a function of adults abundance $A \in [0, +\infty)$

$$\beta \phi(A)$$

where the parameter β is now the *intrinsic fertility* and the function $\phi(\cdot)$ satisfies:

$$\phi(0) = 1, \quad \phi'(A) < 0, \quad \phi(+\infty) = 0. \quad (3.24)$$

With this assumption we introduce a logistic effect because fertility is a decreasing function of adults abundance. Model (3.9) becomes

$$\begin{cases} J_{n+1} = \beta \phi(A_n) A_n \\ A_{n+1} = \sigma_J J_n + \sigma_A A_n. \end{cases} \quad (3.25)$$

For this model the search for equilibria gives the algebraic system

$$\begin{cases} J^* = \beta \phi(A^*) A^* \\ A^* = \sigma_J J^* + \sigma_A A^*, \end{cases} \quad (3.26)$$

and substitution of the first equation into the second yields

$$A^* (1 - \beta \sigma_J \phi(A^*) - \sigma_A) = 0.$$

Thus we have the solution $A^* = 0$ and

$$R_0 \phi(A^*) = 1$$

where we have identified the same basic reproduction number R_0 introduced in the previous model (see (3.14)). This last equation has a solution if and only if $1/R_0$ belongs to the range of the function $\phi(x)$ for $x > 0$, i.e. if and only if the condition $R_0 > 1$ is satisfied. In conclusion we have the equilibria

- $A^* = 0, \quad J^* = 0;$
- $A^* = \phi^{-1}\left(\frac{1}{R_0}\right), \quad J^* = \frac{\beta}{R_0} \phi^{-1}\left(\frac{1}{R_0}\right) = \frac{1 - \sigma_A}{\sigma_J} A^*.$

The non-trivial equilibrium exists if and only if $R_0 > 1$.

Two basic examples for the function $\phi(A)$ are inspired to contest and scramble competition, respectively

$$\phi(A) = \frac{1}{1+A}, \quad (3.27)$$

and

$$\phi(A) = e^{-A}. \quad (3.28)$$

These functions satisfy condition (3.24), and yield respectively

$$A^* = R_0 - 1, \quad \text{and} \quad A^* = \ln(R_0).$$

Concerning stability of these equilibria, the usual linearization procedure gives the linear problem

$$\begin{cases} W_{n+1}^J = K^* W_n^A \\ W_{n+1}^A = \sigma_J W_n^J + \sigma_A W_n^A \end{cases}$$

on the deviations

$$W_n^J = J_n - J^*, \quad W_n^A = A_n - A^*$$

with

$$K^* = \beta (\phi(A^*) + \phi'(A^*)A^*).$$

Notice that, defining $\mathbf{W}_n = (W_n^J, W_n^A)$, one has, analogously to (3.10)

$$\mathbf{W}_{n+1} = A\mathbf{W}_n,$$

where A is exactly like (3.11) with K^* in place of β .

Note that K^* may be negative so that the discussion on the eigenvalues of A may be more complicated than in the case of (3.10). However, we see that for the trivial steady state $J^* = 0$, $A^* = 0$ we have $K^* = \beta$, and we have exactly the case considered before, so that:

the extinction equilibrium $J^* = 0$, $A^* = 0$ is stable if and only if $R_0 < 1$.

Concerning the non trivial equilibrium, the outcome for stability will depend not only on the parameters β , σ_J , σ_A but also on the function $\phi(A)$. For the case (3.27) we have

$$K^* = \frac{\beta}{R_0^2},$$

and the same analysis as in Sect. 3.3 provides the following condition for stability

$$\frac{K^* \sigma_J}{1 - \sigma_A} = \frac{1}{R_0} < 1.$$

Thus we have that:

in the case of (3.27), the non-trivial equilibrium is asymptotically stable whenever it exists (i.e. when $R_0 > 1$).

Considering the case of (3.28), we have

$$K^* = \frac{\beta}{R_0} (1 - \ln R_0) = \frac{1 - \sigma_A}{\sigma_J} (1 - \ln R_0),$$

which can be negative. Reconsidering the eigenvalues

$$\lambda_{\pm} = \frac{1}{2} \left(\sigma_A \pm \sqrt{\sigma_A^2 + 4(1 - \sigma_A)(1 - \ln R_0)} \right),$$

we have to treat separately the two cases of real and complex eigenvalues, namely the two cases

$$\sigma_A^2 + 4(1 - \sigma_A)(1 - \ln R_0) > 0 \text{ and } \sigma_A^2 + 4(1 - \sigma_A)(1 - \ln R_0) < 0$$

respectively corresponding to

$$1 < R_0 < \bar{R}_0 \quad \text{and} \quad R_0 > \bar{R}_0 ,$$

where

$$\bar{R}_0 = e^{\frac{(2-\sigma_A)^2}{4(1-\sigma_A)}} .$$

Actually we have

- $R_0 < \bar{R}_0$
in this case $\lambda_+ > 0$ is the leading eigenvalue and it is easy to see that $\lambda_+ < 1$ if and only if $R_0 > 1$. Thus, in this case the non-trivial equilibrium is asymptotically stable;
- $R_0 > \bar{R}_0$
in this case λ_{\pm} are complex conjugates and

$$|\lambda_{\pm}|^2 = (1 - \sigma_A)(\ln R_0 - 1) < 1$$

if and only if

$$R_0 < R_0^* = e^{\frac{2-\sigma_A}{1-\sigma_A}} .$$

Since $\bar{R}_0 < R_0^*$, the nontrivial equilibrium is stable for $R_0 \in (\bar{R}_0, R_0^*)$ and unstable for $R_0 > R_0^*$. At R_0^* two complex conjugate eigenvalues cross the boundary of the unit circle, the fundamental condition for a Neimarck-Sacker (the equivalent of Hopf for discrete-time systems) bifurcation at R_0^* .

Summarizing we have:

in the case of (3.28), the non-trivial equilibrium is asymptotically stable for $R_0 \in (1, R_0^*)$ and unstable for $R_0 > R_0^*$; at $R_0 = R_0^*$ a Neimarck-Sacker bifurcation occurs, giving rise to quasi-periodic behavior for $R_0 > R_0^*$.

The quasi-periodic behavior means that (J_n, A_n) asymptotically move along a closed curve, without ever exactly repeating themselves, similarly to a particle that rotates of an angle ϑ along a circle, where ϑ is incommensurable with π . An example is given in Fig. 3.11.

We have thus seen that, analogously to Beverton-Holt and Ricker models, when density-dependence arises from contest competition, convergence to equilibrium is ensured, while scramble competition favors oscillatory solutions. However, when we compare the previous analysis to Ricker model, we see that age structure with long-lived adults tends to stabilize the dynamics, so that increasing β causes only quasi-periodic behavior, instead of the period-doubling route to chaos seen in one-dimensional systems.

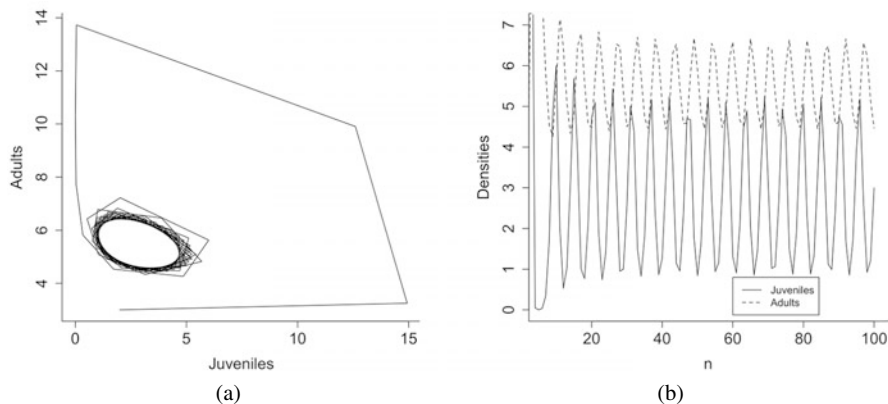


Fig. 3.11 A simulation of model (3.25) with $\phi(A) = e^{-A}$. Parameter values are $\beta = 100$, $\sigma_J = 0.5$, $\sigma_A = 0.75$; initial values $J_1 = 2$, $A_1 = 3$. (a) view on (J, A) phase plane; (b) juvenile and adult densities vs. n , showing the lack of strict periodicity

Problems

3.1. One species growth

Let N_n the population of a species in year n . The dynamics is in discrete time; it is assumed that a fraction σ of the population survives to the following year. Moreover, each individual generates on average $2/(1 + aN_n^2)$ children that survive to the following year: these are then identical to older individuals in terms of birth and death rates. Write down the equation of the model, then:

1. Make the equations non-dimensional reducing the number of parameters.
2. Find the equilibria of the resulting discrete map.
3. Study their stability according to the values of the (reduced) parameters.

3.2. Fitting Ricker model

We estimate the population in a region where it has been recently established to 12 individuals in year 1, 85 in year 2 and 255 in year 3. On the basis of experience in other areas, we have reason to believe that the population follows a dynamics of Ricker type.

1. Estimate the values of α and ν as well as you can, and on that basis predict the population density in year 4. What would then be the equilibrium value of that population? Would that equilibrium be stable?
2. Assume that all estimates can be wrong by 10%. What would then be your uncertainty on the population in year 4?
3. If we assume instead that the population is undergoing Malthusian growth, what could be an estimate for the population in year 4, using the methods presented in Chap. 1?

3.3. Convergence for Beverton-Holt model

Consider the recursive law

$$u_{n+1} = F(u_n), \quad u_0 > 0,$$

where the function $F(\cdot)$ is increasing, concave and such that

$$F(0) = 0, \quad \lim_{u \rightarrow +\infty} F(u) < +\infty.$$

1. Prove that, if $F'(0) < 1$, then no non-trivial equilibrium exists and $\lim_{n \rightarrow +\infty} u_n = 0$.
2. Prove that if $F'(0) > 1$, then a unique non-trivial equilibrium u_∞ exists and $\lim_{n \rightarrow +\infty} u_n = u_\infty$.
3. Prove that the previous results apply to Beverton-Holt model (3.6).

3.4. Beverton-Holt and Verhulst models

Build Beverton-Holt model assuming that the population follows a continuous Verhulst model during the finite time step Δt . Namely obtain model (3.6) by defining

$$N_{n+1} = N(\Delta t)$$

where $N(t)$ is the solution of eq. (1.20) with initial value $N(0) = N_n$. Identify the parameters α and v .

3.5. Eigenvalues of Leslie matrices

Consider a Leslie matrix (3.18), under the assumptions L1)-L3). Show that there exists a positive eigenvalue λ_0 and that all other eigenvalues λ_i satisfy $|\lambda_i| < \lambda_0$. To this aim follow the steps below.

1. By computing $\det(A)$ show that $\lambda = 0$ is not an eigenvalue of A and, writing explicitly the eigenvalue-eigenvector equation $A\mathbf{V} = \lambda\mathbf{V}$, show that (3.20) holds. As necessarily (why?) $V_1 \neq 0$, show that each eigenvalue λ is a root of (3.21).
2. Show that (3.21) has a unique positive solution.
3. Show that each eigenvalue λ (root of (3.21)) satisfies $H(|\lambda|) \geq 1$; hence $|\lambda| \leq \lambda_0$.
4. Take λ eigenvalue with $|\lambda| = \lambda_0$. By using the polar representation of λ and assumption L3), show that necessarily $\lambda = \lambda_0$.

3.6. The Leslie matrix-1

Assume that a population grows according to equation

$$\mathbf{N}_{n+1} = \tilde{A}\mathbf{N}_n$$

where \tilde{A} is a Leslie matrix like (3.18) that does not satisfy all assumptions used in the text. Namely, assume

- $\sigma_1, \sigma_2, \dots, \sigma_{a_+-1} > 0$;
- $\beta_{a_+} = 0$;
- $m = \max\{j : \beta_j > 0\}$.

1. Show that

$$\tilde{A} = \begin{pmatrix} A & 0 \\ B & C \end{pmatrix}$$

where A is an $m \times m$ Leslie-matrix, 0 is an all-zero $m \times (a_+ - m)$ matrix, C is an $(a_+ - m) \times (a_+ - m)$ nilpotent matrix, precisely $C^{a_+ - m} = 0$.

2. Show that, for $n > a_+ - m$, the following holds

$$\tilde{A}^n = \begin{pmatrix} A^n & 0 \\ \sum_{k=0}^{a_+ - m - 1} C^k B A^{n-k-1} & 0 \end{pmatrix}.$$

3. Under the further assumption $\beta_{m-1} > 0$, conclude, using

$$A^n \mathbf{N}_0 \approx \lambda_0^n c_0 v_0$$

where λ_0 is the dominant eigenvalue of A and v_0 is the corresponding eigenvector, that (3.23) holds, even for $j > m$.

4. Explain in words the result obtained through the previous points.

3.7. The Leslie matrix-2

Assume that a population grows according to equation

$$\mathbf{N}_{n+1} = A \mathbf{N}_n$$

where $\mathbf{N}_n \equiv (N_1^n, N_2^n)$ and A is the following 2×2 Leslie matrix :

$$A = \begin{pmatrix} 0 & \beta_2 \\ \sigma_1 & 0 \end{pmatrix}.$$

1. Show that the following holds

$$\mathbf{N}_{2n} \equiv \lambda_0^n \mathbf{N}_0, \quad \mathbf{N}_{2n+1} \equiv \lambda_0^n (k_1 N_2^0, k_2 N_1^0),$$

finding the values of λ_0, k_1, k_2 .

2. Explain why this conclusion is in contrast with the property (3.23).

3. Find a similar example with $n > 2$ and β_j positive in at least two age classes.

3.8. Leslie demography

Consider an age-structured population growing according to a Leslie matrix. Suppose the population is in stable exponential growth (i.e. expression (3.23) holds exactly).

1. Compute the two quantities:

- T_f : the average age of the mothers of all children born at time t ;
- T_m : the average age at which the children born at time t will give birth during their life.

2. Show that $T_f < T_m$ if $\lambda_0 > 1$, and vice versa if $\lambda_0 < 1$.

3. Show that, when $R_0 \approx 1$, (R_0 the reproduction number (3.23)) the following relation holds in first approximation

$$(\lambda_0 - 1)T_m \approx R - 1.$$

3.9. The snow goose dynamics (Modified with permissions from [3])

According to Barrowclough and Rockwell [1], the snow goose (*Anser caurulescens*) has the following demography:

Table 3.1 Snow goose demography according to Barrowclough and Rockwell

i	s	P	z	# number of chicks born alive							
			\Downarrow	0	1	2	3	4	5	6	7
0	0.46	0.00	2	3	0	3	9	3	1	0	0
1	0.76	0.00	3	4	4	6	17	29	11	1	0
2	0.76	0.50	4	12	2	8	25	25	14	5	0
3	0.76	0.86	5	5	1	4	22	37	35	3	2
4-7	0.81	1.00	6	3	1	3	24	36	25	10	0
			7	4	0	2	11	35	21	3	0

In the table to the left, i denotes the age (in years), s the probability of surviving to the following year, P the probability of laying eggs. These probabilities refer to females only and, for simplicity, let us assume that there is 0 probability of surviving to age 8 or beyond.

The table to the right shows, for each age of the mother (z), the number of observed nests with a certain number (between 0 and 7) of chicks born alive. Assume that on average 50% of them will be males, 50% females.

1. On the basis of these data prepare a Leslie matrix for female demography.
2. Compute the expected life of a female at birth, and the expected number of female chicks produced over her life.

3.10. A non-linear Leslie model

Consider an age structured population growing according to a (2-dimensional) non-linear Leslie model. Precisely, letting $u^t = \begin{pmatrix} u_1^t \\ u_2^t \end{pmatrix}$, the model is

$$u^{t+1} = \begin{pmatrix} m_1 & m_2 \\ \psi(N^t)s_1 & 0 \end{pmatrix} u^t$$

where $N^t = u_1^t + u_2^t$, $0 < m_1 < 1$, $0 < s_1 < 1$, $m_2 > 0$ and ψ is a decreasing function such that $\psi(0) = 1$ and $\lim_{N \rightarrow \infty} \psi(N) = 0$.

1. Find the conditions under which this system has a positive equilibrium.
2. Study the conditions for its stability using Jury conditions (see Appendix C, Theorem C.1).

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Stochastic modeling of population growth

*Si la lotería es una intensificación del azar, una periódica infusión del caos en el cosmos, no convendría que el azar interviniera en todas las etapas del sorteo y no en una sola? No es irrisorio que el azar dicte la muerte de alguien y que las circunstancias de esa muerte la reserva, la publicidad, el plazo de una hora o de un siglo—no estén sujetas al azar?*¹

J.L. Borges, “La lotería en Babilonia” in “Ficciones”, 1941

Models so far discussed are all deterministic, meaning that, if the present state were perfectly known, it would be possible to predict exactly all future states. Now we try to face the Babylonian lottery considering models that can describe the possible infusion of chaos (but we would rather say *chance*) into the cosmos, within a probabilistic framework that can take care of all circumstances of events like birth and death.

In fact, we have seen instances (like the discrete logistic) of so-called ‘chaotic’ systems where the determinism becomes weaker, in the sense that any difference, however small, in the initial state would lead to big changes in future states, thus making long-term prediction essentially impossible in such systems: indeed, as any measure of the present state will entail some error, we cannot know exactly the state and thus uncertainty of prediction will grow as the prediction horizon gets longer. However, though long-term prediction may be impossible, in principle such systems follow the paradigm of determinism.

A stochastic model, instead, assigns only a probability distribution to future states. Even if we knew perfectly the present state, we could not predict exactly future states (except for trivial cases; for instance, if a species is extinct, a stochastic model will generally predict that it will be extinct also in the future).

Sometimes the uncertainty may arise from ignorance of many other factors that influence population dynamics, such as the density of other species in the ecosystem, or the genetic composition of a population. In other cases, we may understand the effect of external factors, such as meteorological conditions, but they are essentially unpredictable. In both cases, when (as it is generally the case) a model does not include as variables all factors that affect the dynamics, they may be included,

¹ If the Lottery is an intensification of chance, a periodic infusion of chaos into the cosmos, then is it not appropriate that chance intervene in every aspect of the drawing, not just one? Is it not ludicrous that chance should dictate a person’s death while the circumstances of that death—whether private or public, whether drawn out for an hour or a century—should not be subject to chance? (Translation by Andrew Hurley)

recognizing their potential relevance, as random variables. Or we may dwell on the difference between the statistical regularity of a certain proportion of 50 year old males dying every year, and the unpredictability of which specific individuals will die in the current year. Whatever the fundamental reason, it is clear that in several cases the best we can do is to quantify the uncertainty.

In population biology, two different forms of stochasticity have been extensively examined in models. In the so-called ‘environmental stochasticity’ the demographic rates are allowed to vary unpredictably in time, representing the uncertainty arising, for instance, from climatic factors or variations in the density of species outside the model. Models with environmental stochasticity are generally written in terms of stochastic differential equations, that extend differential equation models such as those examined so far in the book, or that will be seen later. We do not discuss at all this modeling framework in this book, not because we believe there is anything wrong in this approach, but because, in our opinion, no general results of biological interest have arisen so far from the use of stochastic differential equations in ecology.

The other form of stochasticity is the so-called ‘demographic stochasticity’, where the stress is on the fact that biological populations are finite and discrete: they can vary only if one (or more) individuals are born or die or immigrate or emigrate. Hence, while demographic rates represent statistical averages, all demographic events are intrinsically stochastic.

This chapter is devoted to this latter type of modeling and more precisely to birth-and-death processes, i.e. (stationary) Markov processes whose state space are the natural numbers (representing the number of individuals in a population, but also, in other contexts, people in a queue or machines in a production line), and where the only possible transitions (representing births or deaths) are the increase or decrease of one unit in the count of individuals.

Markov processes can be considered as corresponding to ordinary (or partial) differential equations, in the sense that probabilities of future states depend only on present state, and not on past history. A short introduction to the essential properties of Markov processes with countable state space is presented in Appendix D, where some references are also given. Another example of a Markov process is examined in Sect. 8.3 in the context of stochastic epidemic models.

4.1 Birth and death models

Within the stochastic framework, the behavior of a single population is described through a process $N(t)$ in the state space $\mathbb{N} \equiv \{0, 1, \dots\}$. The random variable $N(t)$ denotes the number of individuals of the population at time t and is discrete, while the time variable is continuous. In the process (a birth-and-death process, in fact) the only instantaneous transitions that are allowed are those from a state i to $i + 1$ (a birth), and those from a state i to $i - 1$ (a death). Precisely, we will assume that:

$$\begin{aligned}
& \bullet \quad \mathbb{P}(N(t+h) = i+1 \mid N(t) = i) = \lambda_i h + o(h); \\
& \bullet \quad \mathbb{P}(N(t+h) = i-1 \mid N(t) = i) = \mu_i h + o(h); \\
& \bullet \quad \sum_{j: |j-i| > 1} \mathbb{P}(N(t+h) = j \mid N(t) = i) = o(h);
\end{aligned} \tag{4.1}$$

where $\{\lambda_i\}$ and $\{\mu_i\}$ are sequences of nonnegative coefficients, while $o(h)$ represents any function such that

$$\lim_{h \rightarrow 0} \frac{o(h)}{h} = 0.$$

It is not possible that $N(t)$ becomes negative, hence it is necessary to assume that $\mu_0 = 0$. The other coefficients are free to have any value, though we will discuss how to assign them in a way that reproduces biological features similarly to what is accomplished in deterministic models.

In particular, we will consider two main population processes, first the linear birth-and-death process corresponding to the deterministic Malthus model:

$$\textbf{Malthus model:} \quad \lambda_i = \lambda i \quad \mu_i = \mu i \tag{4.2}$$

where λ and μ are positive constants. Then the non-linear case equivalent to the deterministic logistic model:

$$\textbf{logistic model:} \quad \lambda_i = \lambda i \quad \mu_i = \mu i + \nu i^2 \tag{4.3}$$

where the constants λ, μ, ν are positive.

Conditions (4.1) can be considered as representing, in a semi-intuitive way, a Markov process having as infinitesimal transition rates

$$q_{i,i+1} = \lambda_i, \quad q_{i,i-1} = \mu_i, \quad q_{ii} = -(\lambda_i + \mu_i), \quad q_{ij} = 0 \text{ if } |i-j| > 1.$$

In Appendix D it is discussed how to build a (minimal) Markov process $N(t)$ with a given matrix Q of infinitesimal transition rates. The corresponding matrix of *transition probabilities* $P(t)$ has elements

$$P_{ij}(t) = \mathbb{P}(N(t) = j \mid N(0) = i).$$

The condition

$$\lambda_i \leq a + bi, \quad i \in \mathbb{N}$$

where a and b are nonnegative constants avoids “explosions in finite time” and ensures that the birth-and-death process is defined for all $t \geq 0$ satisfying

$$\sum_{j=0}^{\infty} P_{ij}(t) = 1 \quad \text{for all } t \geq 0, i \in \mathbb{N}.$$

The matrix P satisfies the so-called *Chapman-Kolmogorov equations*:

$$P_{ij}(t+s) = \sum_{k \in E} P_{ik}(t)P_{kj}(s) \quad \text{for all } i, j \in \mathbb{N}, \quad t, s \geq 0. \quad (4.4)$$

Intuitively, the equations state that for going from i to j in time $t+s$, the process will move to some k in time t , and then from k to j in time s .

Furthermore, the matrix $P(t)$ satisfies two systems of (linear) differential equations, the backward and forward Kolmogorov equations; the former, given by eq. (D.1), become for a birth-and-death process

$$P'_{ij}(t) = \lambda_i P_{i+1,j}(t) + \mu_i P_{i-1,j}(t) - (\lambda_i + \mu_i) P_{ij}(t) \quad i, j \in \mathbb{N}. \quad (4.5)$$

The set of equations (4.5) can be seen, for each j (that can be considered as a parameter), as a (finite or infinite) system of equations in the unknowns P_{ij} , $i \in \mathbb{N}$. It can be written in matrix notation as

$$P'(t) = QP(t)$$

where Q is the matrix of infinitesimal transition rates. The Kolmogorov forward equations (D.2) become for a birth-and-death process

$$P'_{ij}(t) = \lambda_{j-1} P_{i,j-1}(t) + \mu_{i+1} P_{i,j+1}(t) - (\lambda_i + \mu_i) P_{ij}(t) \quad i, j \in \mathbb{N} \quad (4.6)$$

or, in matrix notation, $P'(t) = P(t)Q$. Now i can be taken as a parameter and the unknowns are P_{ij} , $j \in \mathbb{N}$.

4.2 Stationary distribution

An interesting question is whether a birth-and-death process has a stationary distribution, i.e. a distribution such that, if the process follows the stationary distribution at time $t = 0$, it will follow the same distribution at any time $t > 0$. We may say that a stationary distribution corresponds to an equilibrium of a deterministic system (and is also attracting; see Theorem D.1 of Appendix D).

Results will be fundamentally different according to whether it is assumed that $\lambda_0 > 0$ (which may seem odd if one thinks of actual births, but may be sensible if immigration from outside is considered) or $\lambda_0 = 0$ (when the population reaches size 0, no births are possible; hence the population will be extinct forever).

In the first case, that implies that immigration from outside occurs, all states are in the same communicating class and it is possible that a non-trivial stationary distribution exists.

In the second case, when the population is extinct, it will be extinct forever. In mathematical terms 0 is an *absorbing state*. It can be proved that all other states are in the same transient class, and an important question is determining the probability of extinction, and the mean time before extinction.

Looking for stationary solutions, we assume

$$\lambda_i > 0 \quad \text{for all } i \geq 0 \quad \text{and} \quad \mu_i > 0 \quad \text{for all } i \geq 1.$$

We recall, as shown in Appendix D, that the most convenient condition to check whether $\{\pi_i\}_{i \in E}$ is a stationary solution is (D.5), i.e.

$$\sum_{i \in E} \pi_i q_{ij} = 0 \quad \forall j \in E.$$

For a birth-and-death process, they become

$$\begin{aligned} -\lambda_0 \pi_0 + \mu_1 \pi_1 &= 0, \\ \lambda_{i-1} \pi_{i-1} - (\lambda_i + \mu_i) \pi_i + \mu_{i+1} \pi_{i+1} &= 0 \quad i \geq 1. \end{aligned} \tag{4.7}$$

It is easier to find the solution of (4.7) through the so-called *detailed balance equations*

$$\lambda_i \pi_i = \mu_{i+1} \pi_{i+1}. \tag{4.8}$$

In fact:

a solution of (4.7) satisfies eqs. (4.8) and vice versa.

This can be proved by induction because for a solution of (4.7) Equation (4.8) is true for $i = 0$ (it is the first of (4.7)) and, assuming that (4.8) holds for $i - 1$, from the first of (4.7), we obtain

$$\mu_{i+1} \pi_{i+1} = (\lambda_i + \mu_i) \pi_i - \lambda_{i-1} \pi_{i-1} = \lambda_i \pi_i$$

where the last equality comes from the inductive hypothesis. The vice versa is obvious.

Note that the detailed balance equations (4.8) can be interpreted as saying that, at the stationary distribution, the rate at which the process moves (through births) from i to $i + 1$ must be equal to the rate at which the process moves (through deaths) from $i + 1$ to i .

From (4.8), one immediately has

$$\pi_1 = \frac{\lambda_0}{\mu_1} \pi_0 \quad \text{and iteratively} \quad \pi_n = \frac{\lambda_0 \cdots \lambda_{n-1}}{\mu_1 \cdots \mu_n} \pi_0.$$

One can then find π_0 from the condition that $\sum_{n=0}^{\infty} \pi_n = 1$.

Setting

$$\rho_n = \frac{\lambda_0 \cdots \lambda_{n-1}}{\mu_1 \cdots \mu_n} \quad \text{with} \quad \rho_0 = 1,$$

the condition becomes

$$\pi_0 \sum_{n=0}^{\infty} \rho_n = 1.$$

Hence there are two possibilities:

- if $\sum_{n=0}^{\infty} \rho_n < \infty$, then

$$\pi_0 = \frac{1}{\sum_{n=0}^{\infty} \rho_n}, \quad \pi_i = \frac{\rho_i}{\sum_{n=0}^{\infty} \rho_n} \quad i > 0,$$

is the unique stationary distribution;

- if $\sum_{n=0}^{\infty} \rho_n = \infty$, there are no stationary distributions.

As a simple example, let us consider the Malthus model (4.2) with immigration (thus the equivalent of model (1.9)), namely a birth and death process, where there is a fixed immigration rate α , and every individual has fixed birth rate β and death rate μ , independently of population density. This translates into the assumptions:

$$\lambda_n = \alpha + \beta n \quad \mu_n = \mu n.$$

In order to study the convergence of the series $\sum_n \rho_n$, it is convenient using the ratio criterion. Then

$$\frac{\rho_{n+1}}{\rho_n} = \frac{\lambda_n}{\mu_{n+1}} = \frac{\alpha + \beta n}{\mu(n+1)}. \quad (4.9)$$

Letting n go to ∞ in (4.9), one sees that

- if $\beta < \mu$, $\lim_{n \rightarrow \infty} \frac{\rho_{n+1}}{\rho_n} < 1$, so the series converges, and there exists a unique stationary distribution;
- if $\beta > \mu$, $\lim_{n \rightarrow \infty} \frac{\rho_{n+1}}{\rho_n} > 1$, so the series diverges, and there are no stationary distributions.

The case $\beta = \mu$ cannot be handled in the previous method. In this case, computing directly ρ_n and using the inequality $\alpha + \beta j > \beta j$, one has

$$\rho_n = \frac{\alpha(\alpha + \beta) \cdots (\alpha + \beta(n-1))}{\mu^n n!} > \frac{\alpha \beta^{n-1} (n-1)!}{\mu^n n!} = \frac{\alpha}{\mu n}$$

so that $\sum_n \rho_n$ diverges, being larger than the harmonic series, and there are no stationary distributions.

Summarizing, one may see these results as exactly corresponding to those obtained in Sect. 1.3:

for the Malthus model with immigration, a unique stationary distribution exists, if and only if $\beta < \mu$.

4.3 Probability of extinction

We assume

$$\lambda_0 = 0, \quad \lambda_i + \mu_i > 0 \quad \text{for all } i \geq 1.$$

The first condition implies that 0 is an absorbing state (if $N(T) = 0$, then $N(t) = 0$ for all $t \geq T$), the second means that there are no other absorbing states.

We want to compute the *absorption probability*

$$u_i = \mathbb{P}(N(T) = 0 \text{ for some } T > 0 \mid N(0) = i).$$

We compute this by considering the embedded jump Markov chain Z_n , i.e. we compute

$$u_i = \mathbb{P}(Z_n = 0 \text{ for some } n > 0 \mid Z_0 = i).$$

Since $N(t)$ is a birth-and-death process, Z_n can jump only 1 unit upwards or downwards; in other words Z_n is a random walk with

$$\mathbb{P}(Z_{n+1} = i+1 \mid Z_n = i) = p_i \quad \mathbb{P}(Z_{n+1} = i-1 \mid Z_n = i) = q_i \quad i \geq 1,$$

where

$$p_i = \frac{\lambda_i}{\lambda_i + \mu_i}, \quad q_i = 1 - p_i = \frac{\mu_i}{\lambda_i + \mu_i}. \quad (4.10)$$

The classical random walk occurs when $p_i \equiv p$ and necessarily $q_i \equiv q = 1 - p$.

Let us first compute

$$u_i = \mathbb{P}(Z_n \text{ hits } 0 \mid Z_0 = i) = \mathbb{P}(\text{it exists } n \geq 0 \text{ s.t. } Z_n = 0 \mid Z_0 = i).$$

By conditioning on the first step, and using the Markov property one has

$$u_i = p_i \mathbb{P}(Z_n \text{ hits } 0 \mid Z_1 = i+1) + q_i \mathbb{P}(Z_n \text{ hits } 0 \mid Z_1 = i-1).$$

By shifting the time origin, it is clear that

$$\mathbb{P}(Z_n \text{ hits } 0 \mid Z_1 = i + 1) = u_{i+1}$$

so that the equation reduces to

$$u_i = p_i u_{i+1} + q_i u_{i-1}, \quad i = 1, \dots \quad (4.11)$$

This is an infinite system of linear equations to which the obvious conditions

$$u_0 = 1$$

has to be added; still, it may have infinitely many solutions.

In order to proceed, we employ the following result (see, e.g., [4, Theorem 3.3.1]): $\mathbb{P}(Z_n \text{ hits } 0 \mid Z_0 = i)$ is equal to u_i , the smallest positive solution of (4.11).

Now set $w_i = u_i - u_{i+1}$ ($i = 0, \dots$), so that (4.11) can be rewritten as

$$p_i w_i = q_i w_{i-1} \implies w_i = \frac{q_i \cdots q_1}{p_i \cdots p_1} w_0 = \prod_{j=1}^i \frac{q_j}{p_j} w_0. \quad (4.12)$$

From w_j 's, we can compute

$$1 - u_i = (u_0 - u_1) + \cdots + (u_{i-1} - u_i) = \sum_{j=0}^{i-1} w_j = w_0 \sum_{j=0}^{i-1} \prod_{l=1}^j \frac{q_l}{p_l}$$

or

$$u_i = 1 - w_0 \sum_{j=0}^{i-1} \prod_{l=1}^j \frac{q_l}{p_l}. \quad (4.13)$$

(4.13) yields a solution of (4.11) for any choice of $w_0 = 1 - u_1$. We need to find the minimal nonnegative solution.

$$\text{Assume} \quad \sum_{j=0}^{\infty} \prod_{i=1}^j \frac{q_i}{p_i} = +\infty.$$

If $w_0 > 0$, then (4.13) yields negative values for i large enough, hence it is not acceptable. We are then left with the choice $w_0 = 0$, i.e. $u_i \equiv 1$.

$$\text{Let instead} \quad \sum_{j=0}^{\infty} \prod_{i=1}^j \frac{q_i}{p_i} < +\infty.$$

Then we can set

$$w_0 = \frac{1}{\sum_{j=0}^{\infty} \prod_{i=1}^j \frac{q_i}{p_i}}$$

and (4.13) yields

$$u_i = 1 - \frac{\sum_{j=0}^{i-1} \prod_{l=1}^j \frac{q_l}{p_l}}{\sum_{j=0}^{\infty} \prod_{i=1}^j \frac{q_i}{p_i}} \quad (4.14)$$

which satisfies $0 < u_i < 1$ for all i .

If we chose w_0 smaller, then we would obtain u_i larger than (4.14): in this way we cannot obtain the minimal solution. On the other hand, if w_0 were larger, u_i would become negative for large i .

We have thus established the following dichotomy:

- if

$$\sum_{i=0}^{\infty} \prod_{j=1}^i \frac{q_j}{p_j} = +\infty \quad (4.15)$$

then $u_i \equiv 1$ for all $i \in \mathbb{N}$;

- if the sum in (4.15) is finite, then u_i is given by expression (4.14).

The simplest case is that of a standard random walk, $p_i \equiv p$, in which case one sees that

$$u_i = \begin{cases} 1 & \text{if } q \geq p \\ \left(\frac{q}{p}\right)^i & \text{if } q < p. \end{cases} \quad (4.16)$$

In words, the probability of ever hitting 0 is 1, if the probability of moving to the left is greater or equal than the probability of moving to the right. Instead, if the probability of moving to the right is greater than the probability of moving to the left, there is a positive probability that the random walk will drift to infinity without ever hitting 0.

We can apply the previous general results to the specific population models (4.2) and (4.3). First we consider the Malthus model. As seen above in (4.10), Z_n is a random walk with

$$p_i = \frac{\lambda_i}{\lambda_i + \mu_i} = \frac{\lambda}{\lambda + \mu} \quad q_i = \frac{\mu_i}{\lambda_i + \mu_i} = \frac{\mu}{\lambda + \mu}.$$

Hence from (4.16), we have:

for the Malthus model (4.2) the probability of extinction is given by

$$u_i = \begin{cases} 1 & \text{if } \mu \geq \lambda \iff R_0 \leq 1 \\ \left(\frac{\mu}{\lambda}\right)^i = R_0^{-i} & \text{if } \mu < \lambda \iff R_0 > 1 \end{cases} \quad (4.17)$$

using the definition (1.6) of the reproduction ratio R_0 .

Note that $u_i = (u_1)^i$, as it can be justified intuitively. Indeed, since in this model birth and death rate of each individual are not influenced by how many other individuals are present, the progenies of each initial individual develop independently

of one another. Hence, the probability u_i that a population starting from i individuals gets extinct (i.e. the probability that each progeny gets extinct) is equal to the product of the probability that each family-tree descending from one of the i initial individuals gets extinct, i.e. $(u_1)^i$.

As a second example, we consider the logistic model (4.3). In this case Z_n has probabilities

$$p_i = \frac{\lambda}{\lambda + \mu + \nu i} \quad q_i = \frac{\mu + \nu i}{\lambda + \mu + \nu i}.$$

It is then easy to see that condition (4.15) holds, so that:

for the logistic model (4.3) extinction is certain starting from any initial population i .

A similar property holds for any model in which the growth rate becomes negative at high densities (see Problem 4.3): a sufficient condition for this is

$$\lambda_i \leq \eta \mu_i \quad \text{for } i \text{ large enough, with } \eta < 1.$$

This conclusion says that any population with a demography of generalized logistic type is doomed to extinction. The next section qualifies this statement by analyzing how long we expect to wait for extinction to occur.

4.4 Time to extinction

For populations such that extinction is certain, one can compute the mean time to extinction. This can be obtained following the same arguments as in the previous section; however, the time to transitions has to be taken into account.

Let τ the random variable denoting the time to extinction, i.e.

$$\tau = \inf\{t : N(t) = 0\}$$

and let $W_i = \mathbb{E}(\tau | N(0) = i)$. Consider now T_1 the time of the first transition (see Appendix D) and condition on the value of $N(T_1)$. We obtain

$$\begin{aligned} W_i = \mathbb{E}(T_1 | N(0) = i) &+ p_i \mathbb{E}(\tau - T_1 | N(0) = i, N(T_1) = i + 1) \\ &+ q_i \mathbb{E}(\tau - T_1 | N(0) = i, N(T_1) = i - 1) \end{aligned}$$

where p_i is the probability (already computed) that the first transition is to the right, while $q_i = 1 - p_i$ is the probability that the first transition is to the left.

By the (strong) Markov property and the time-homogeneity of transitions, $N(t - T_1)$ is distributed like $N(t)$ conditional on the initial condition, hence

$$\mathbb{E}(\tau - T_1 | N(0) = i, N(T_1) = i + 1) = \mathbb{E}(\tau | N(0) = i + 1) = W_{i+1}.$$

The previous equation can then be written as

$$W_i = \frac{1}{\lambda_i + \mu_i} + \frac{\lambda_i}{\lambda_i + \mu_i} W_{i+1} + \frac{\mu_i}{\lambda_i + \mu_i} W_{i-1}, \quad i \geq 1. \quad (4.18)$$

A boundary condition is clearly $W_0 = 0$, but we are now left with an infinite system of linear equation. We refer to [4, Theorem 3.3.3] for the following result:

$$\mathbb{E}(\tau | N(0) = i) \text{ is the minimal nonnegative solution } W_i \text{ of (4.18).}$$

Let us apply this result to the Malthusian case (4.2), assuming $\lambda \leq \mu$, because we saw before that for $\lambda > \mu$ extinction is not certain. Equation (4.18) becomes

$$(\lambda + \mu)W_i = \frac{1}{i} + \lambda W_{i+1} + \mu W_{i-1}. \quad (4.19)$$

Introducing $U_i = W_{i+1} - W_i$, this becomes

$$U_i = \frac{\mu}{\lambda} U_{i-1} - \frac{1}{\lambda i}, \quad (4.20)$$

from which recursively one obtains

$$U_i = \left(\frac{\mu}{\lambda}\right)^i U_0 - \sum_{j=1}^i \left(\frac{\mu}{\lambda}\right)^{i-j} \frac{1}{\lambda j} = \left(\frac{\mu}{\lambda}\right)^i \left(U_0 - \sum_{j=1}^i \left(\frac{\lambda}{\mu}\right)^j \frac{1}{\lambda j} \right), \quad (4.21)$$

for $i \geq 1$. Since we still don't know $U_0 = W_1$, letting i go to infinity in the term in brackets in the rightmost term in (4.21), we have two possibilities that we consider below.

Case 1. A first possibility corresponds to

$$\sum_{j=1}^{+\infty} \left(\frac{\lambda}{\mu}\right)^j \frac{1}{\lambda j} = +\infty.$$

The series diverges for $\lambda \geq \mu$; since we suppose $\lambda \leq \mu$, this case occurs for $\lambda = \mu$.

Given any choice of $U_0 > 0$, we would obtain

$$\sum_{j=1}^i \left(\frac{\lambda}{\mu}\right)^j \frac{1}{\lambda j} > U_0,$$

for i large enough, and thus $U_i < 0$ for i large. This is inconsistent probabilistically (it cannot be $\mathbb{E}(\tau | N(0) = i+1) < \mathbb{E}(\tau | N(0) = i)$) and would also lead to have $W_k < 0$ for k large enough.

The only possibility is then $U_0 = +\infty$, i.e. $W_1 = +\infty$. This means that the expected time to extinction starting with 1 individual (and thus with more than 1 individual) is infinite.

Case 2. The other option

$$\sum_{j=1}^{+\infty} \left(\frac{\lambda}{\mu}\right)^j \frac{1}{\lambda j} < +\infty,$$

implies that any choice of

$$U_0 \geq \sum_{j=1}^{+\infty} \left(\frac{\lambda}{\mu}\right)^j \frac{1}{\lambda j}$$

would lead to positive values of U_i and thus of W_i for all i . However, we had stated before that the expected time is given by the minimal nonnegative solution of (4.18), that is attained when

$$U_0 = \sum_{j=1}^{+\infty} \left(\frac{\lambda}{\mu}\right)^j \frac{1}{\lambda j}.$$

In this case ($\lambda < \mu$) we thus have

$$\begin{aligned} U_0 = \mathbb{E}(\tau \mid N(0) = 1) &= \sum_{j=1}^{+\infty} \left(\frac{\lambda}{\mu}\right)^j \frac{1}{\lambda j} = \frac{1}{\lambda} \sum_{j=1}^{+\infty} \int_0^{\lambda/\mu} x^{j-1} dx \\ &= \frac{1}{\lambda} \int_0^{\lambda/\mu} \sum_{j=1}^{+\infty} x^{j-1} dx = \frac{1}{\lambda} \int_0^{\lambda/\mu} \frac{1}{1-x} dx \\ &= -\frac{1}{\lambda} \log \left(1 - \frac{\lambda}{\mu}\right) = \frac{1}{\lambda} \log \left(\frac{\mu}{\mu - \lambda}\right). \end{aligned} \tag{4.22}$$

Summarizing we have:

for the stochastic Malthus model (4.2), the expected time of extinction is

- $\mathbb{E}(\tau \mid N(0) = i) = +\infty$ if $\lambda = \mu$;
- $\mathbb{E}(\tau \mid N(0) = 1) = \frac{1}{\lambda} \log \left(\frac{\mu}{\mu - \lambda}\right)$ if $\lambda < \mu$.

In order to get a feeling for the result, we show in Fig. 4.1 the expected time to extinction scaled in terms of the mean length of life of individuals, $\mathbb{E}(L) = 1/\mu$.

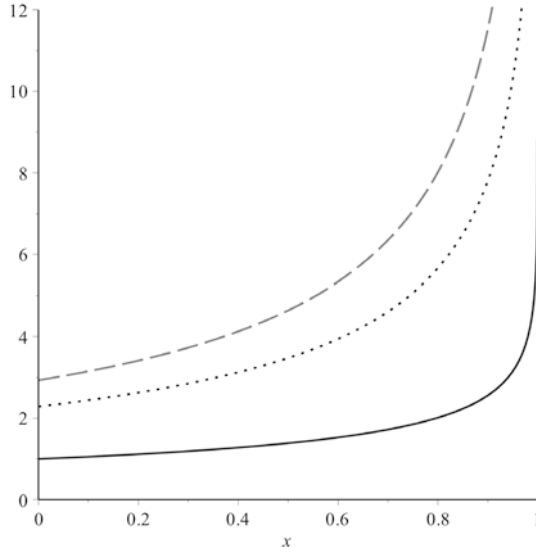


Fig. 4.1 Mean extinction time, measured in units of mean life length, for the birth-and-death process (4.2) as a function of $x = \frac{\lambda}{\mu} \leq 1$. The solid line corresponds to initial population size $i = 1$; the dotted to $i = 5$; the dashed to $i = 10$

We thus have

$$\frac{\mathbb{E}(\tau \mid N(0) = i)}{\mathbb{E}(L)} = \begin{cases} \frac{\mu}{\lambda} \log \left(\frac{1}{1 - \frac{\lambda}{\mu}} \right), & i = 1 \\ \sum_{j=0}^{i-1} \mu U_j \quad \text{with } U_j \text{ in (4.21)}, & i > 1 \end{cases}$$

that can be seen as a function of μ/λ and of the initial population i .

One can see that when $\lambda = 0$ and $i = 1$, the expected time to extinction is equal to the mean life of an individual (which is obvious) but increasing λ and i does not increase $\mathbb{E}(\tau)$ much until λ becomes almost equal to μ .

In principle, one could compute mean extinction time, even when extinction is not certain. In that case, in order to obtain relevant results, one would have to condition on the fact that extinction does occur, computing $\mathbb{E}(\tau \mid N(0) = i, \tau < +\infty)$. The results can be obtained in a way similar to above, but taking the conditioning into account (see Problem 4.5).

4.5 Extinction time with a bound on population size

We have seen that, when the demographic rates are of logistic type (see (4.3) and the Remark below it), extinction is certain. However, it may be that the average time to extinction is so large, that we can neglect extinction over practical time horizons.

As studying extinction time for model (4.3) is rather complicated (see [5] for some examples), we consider here a variant that can be easily analyzed. Precisely, we assume that there exists an upper barrier that cannot be passed, and that the demography is Malthusian below the barrier; namely we assume

$$\lambda_i = \begin{cases} \lambda i & \text{if } i < K \\ 0 & \text{if } i \geq K \end{cases}, \quad \mu_i = \mu i. \quad (4.23)$$

Once the process reaches state K it will stay there until a transition brings it back to the state $K - 1$.

Now (4.18) becomes

$$(\lambda + \mu)W_i = \frac{1}{i} + \lambda W_{i+1} + \mu W_{i-1} \quad 1 \leq i \leq K - 1$$

to which one must add $W_0 = 0$ and $W_K = \frac{1}{\mu K} + W_{K-1}$.

Passing to the variables U_i , the last condition means $U_{K-1} = \frac{1}{\mu K}$. Since (4.21) is still valid for $1 \leq i \leq K - 1$, one obtains

$$\frac{1}{\mu K} = \left(\frac{\mu}{\lambda}\right)^{K-1} U_0 - \sum_{j=1}^{K-1} \left(\frac{\mu}{\lambda}\right)^{K-1-j} \frac{1}{\lambda j}$$

i.e.

$$W_1 = U_0 = \sum_{j=1}^{K-1} \left(\frac{\lambda}{\mu}\right)^j \frac{1}{\lambda j} + \left(\frac{\lambda}{\mu}\right)^{K-1} \frac{1}{\mu K} = \sum_{j=1}^K \left(\frac{\lambda}{\mu}\right)^j \frac{1}{\lambda j}. \quad (4.24)$$

Thus, $\mathbb{E}(\tau \mid N(0) = 1) = W_1 = U_0$ is given by the first K terms of a series that is convergent if $\lambda < \mu$ and divergent for $\lambda \geq \mu$; this observations means that, when $\lambda \geq \mu$, W_1 grows to infinity as K is increased. An asymptotic expansion makes it possible to quantify this statement. Again we consider μW_1 , i.e. the average extinction time measured in average life lengths.

For $\lambda < \mu$, (4.24) are the first terms of a convergent series, so that μW_1 can be approximated by its sum, i.e. (4.22).

On the other hand, for $\lambda = \mu$, W_1 is given by the first terms of the harmonic series. Hence, its asymptotic expansion is well known:

$$\mu W_1 \approx (\log(K) + \gamma) \quad (4.25)$$

where $\gamma \approx 0.5772$ is Euler's constant.

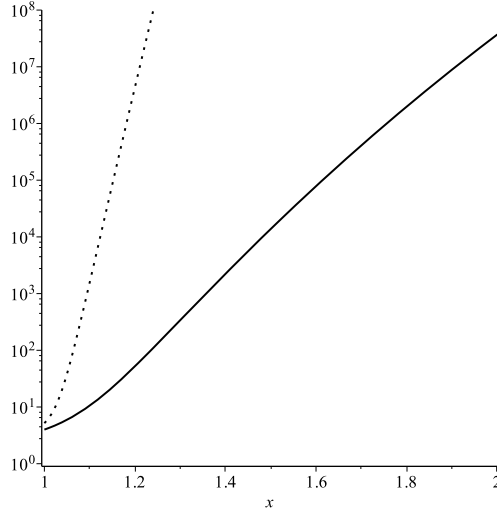


Fig. 4.2 Mean extinction time, measured in units of mean life length, for the birth-and-death process (4.23) as a function of $x = \frac{\lambda}{\mu} \geq 1$. The solid line corresponds to $K = 30$; the dotted to $K = 100$

Finally, when $\lambda > \mu$, one obtains

$$\begin{aligned} \mu W_1 &= \left(\frac{\lambda}{\mu}\right)^K \sum_{j=1}^K \left(\frac{\lambda}{\mu}\right)^{j-K-1} \frac{1}{j} = \left(\frac{\lambda}{\mu}\right)^{K-1} \sum_{l=0}^{K-1} \left(\frac{\mu}{\lambda}\right)^l \frac{1}{(K-l)} \\ &\approx \frac{1}{K} \left(\frac{\lambda}{\mu}\right)^{K-1} \sum_{l=0}^{\infty} \left(\frac{\mu}{\lambda}\right)^l = \frac{1}{(1 - \frac{\mu}{\lambda})K} \left(\frac{\lambda}{\mu}\right)^{K-1}. \end{aligned}$$

This means that the mean extinction time grows exponentially with K , precisely W_1 grows like $e^{\alpha K}/K$ where $\alpha = \log(\lambda/\mu)$. Thus it becomes astronomically large for moderate K (see Fig. 4.2).

4.6 Relations with deterministic processes

In the case of the linear birth-and-death process (4.2), relative to the Malthus model, consider the expected value of population size at time t

$$m_i(t) = \mathbb{E}(N(t) \mid N(0) = i) = \sum_{j=0}^{\infty} j P_{i,j}(t). \quad (4.26)$$

Using Kolmogorov forward equations (4.6), and interchanging derivative and (infinite) sums (this could be rigorously justified by first showing that the series converge

absolutely), one obtains

$$\begin{aligned}
 m'_i(t) &= \sum_{j=0}^{\infty} j P'_{i,j}(t) = \sum_{j=0}^{\infty} j [P_{i,j+1}(j+1)\mu + P_{i,j-1}(j-1)\lambda - P_{i,j}j(\lambda + \mu)] \\
 &= \sum_{k=1}^{\infty} \mu(k-1)kP_{i,k} + \sum_{k=0}^{\infty} \lambda(k+1)kP_{i,k} - \sum_{j=0}^{\infty} (\lambda + \mu)j^2 P_{i,j} \\
 &= \sum_{k=1}^{\infty} (\lambda - \mu)kP_{i,k} = (\lambda - \mu)m_i(t)
 \end{aligned} \tag{4.27}$$

(4.27) shows that the expected value of the process follows Malthus equation with parameter $r = \lambda - \mu$, so that

$$m_i(t) = ie^{(\lambda - \mu)t}.$$

This formula can be contrasted with (4.17). If $\lambda > \mu$, the expected value of the population grows exponentially; still extinction may be likely. To give a numerical example, if $\lambda = 1$ and $\mu = 0.9$, and the initial value is 1 individual, the expected value of the population at time $t = 100$ is $e^{10} \approx 22 \times 10^3$, but the probability of extinction is $9/10$; furthermore, we can be practically certain that, if extinction occurs at all, it must have occurred within time $t = 100$. Thus, there is 90 % probability that the population will be extinct, but its expected values is very large, meaning that, conditional on non-extinction, the expected population size will be around 2×10^5 .

Note that the Malthusian growth rate depends on the difference $\lambda - \mu$, while the extinction probability depends on the ratio μ/λ . Thus, populations with the same expected growth rate may have very different extinction probability.

The fact that the expected value of the stochastic model coincides with the value of the deterministic model holds only for the linear case (4.2). In general, they differ, and the fundamental reason for this is that $\mathbb{E}(f(X)) \neq f(\mathbb{E}(X))$ unless f is linear.

One may wonder whether there is then any general relation between stochastic and deterministic models. Indeed, there is one and basically it follows from the law of large numbers: as the number of trials grows to infinity, the fraction of successes converges to the expected value.

In this context, the problem requires mathematical techniques much beyond the level of this text. However, it is possible to quote a result of [2]), that have actually handled more general cases and obtained much more detailed results. We assume that there exists a typical scale K of the population (it may represent habitat size), and that the parameters of the birth-and-death process depend on K as

$$\lambda_i^{(K)} = Kb \left(\frac{i}{K} \right), \quad \mu_i^{(K)} = Km \left(\frac{i}{K} \right) \tag{4.28}$$

where b and m are given functions.

For instance, logistic growth could be represented by

$$\lambda_i^{(K)} = \lambda i, \quad \mu_i^{(K)} = i \left(\mu + v \frac{i}{K} \right) \quad (4.29)$$

where $v \frac{i}{K}$ represents the extra mortality to crowding. In this case, we would have

$$b(x) = \lambda x \quad \text{and} \quad m(x) = x(\mu + vx) .$$

The following result (a special case of Theorem 8.8.1 from [2]), represents a law of large number for this case:

let $N^{(K)}(t)$ be a family of birth-and-death process, with rates given by (4.28). Let $F(x) = b(x) - m(x)$ be a Lipschitz function on \mathbb{R}_+ . Let

$$\lim_{K \rightarrow \infty} \frac{N^{(K)}(0)}{K} = n_0 \geq 0 \quad \text{w.p. 1.}$$

Then for all $T > 0$,

$$\lim_{K \rightarrow \infty} \sup_{t \in [0, T]} \left| \frac{N^{(K)}(t)}{K} - n(t) \right| = 0 \quad \text{w.p. 1} \quad (4.30)$$

where $n(t)$ is the solution of the Cauchy problem

$$\begin{cases} n'(t) = F(n(t)) \\ n(0) = n_0 . \end{cases} \quad (4.31)$$

In words, we can say that, as the scale of the population grows to infinity, the stochastic model converges (technically, it is an almost-everywhere convergence) to the deterministic model, uniformly in any finite interval $[0, T]$.

Several aspects of (4.30) can be noted. First of all, if $n_0 > 0$, this means that the initial condition $N^{(K)}(0) = O(K)$, i.e. it is very large. The approximation of the stochastic model with eq. (4.31) works well when K is large, as well as the initial condition $N^{(K)}(0)$.

If instead $N^{(K)}(0)$ is kept fixed (as K increases) at some (small) value (the situation considered when looking at extinction probabilities), we have

$$\lim_{K \rightarrow \infty} \frac{N^{(K)}(0)}{K} = 0 .$$

Then, if we assume $\lambda_0^{(K)} = 0$ (extinction is possible), $n(t) \equiv 0$. This is not a useful information, because it does not allow to distinguish between the cases in which $N^{(K)}(T) = 0$ and those in which $N^{(K)}(T) > 0$ and the population will continue growing. The techniques of Sect. 4.3 are required to study the probability of extinction.

Moreover, in the same section, we have shown that, when birth and death rates follow the logistic-like rule (4.29), then $\lim_{t \rightarrow +\infty} N^{(K)}(t) = 0$, however large is K . On the other hand, it is easy to show that (if $\lambda > \mu$)

$$\lim_{t \rightarrow +\infty} x(t) = \frac{\lambda - \mu}{\nu},$$

that represents the carrying capacity for the deterministic equation. This shows that we cannot interchange limits:

$$0 = \lim_{K \rightarrow \infty} \lim_{t \rightarrow +\infty} \frac{N^{(K)}(t)}{K} \neq \lim_{t \rightarrow +\infty} \lim_{K \rightarrow \infty} \frac{N^{(K)}(t)}{K} = \frac{\lambda - \mu}{\nu}.$$

Equation (4.31) describes accurately the stochastic model (under the assumptions of the previous Theorem) only for finite intervals of time, while it is certain that sooner or later the stochastic model will randomly drift to extinction. However, the time scale of these fluctuations may be so large (see the computation in Sect. 4.5) to be irrelevant from a practical point of view.

Figure 4.3 shows some simulations of model (4.29) that exhibit some typical features. Some simulations undergo early extinction; the probability of this event can be approximated very well by (4.17): for the parameter values used in the figure, this amounts to 0.5.

Those that do not undergo early extinction fluctuate around the equilibrium of the differential equations. The simulations are not very close to the solution of the differential equation, as the previous theorem suggests, as that is a limiting theorem as a scale parameter (in this case K) goes to infinity, while here $K = 30$ definitely is not very large. Other results, obtained by Kurtz and co-workers in [2, 3], provide cen-

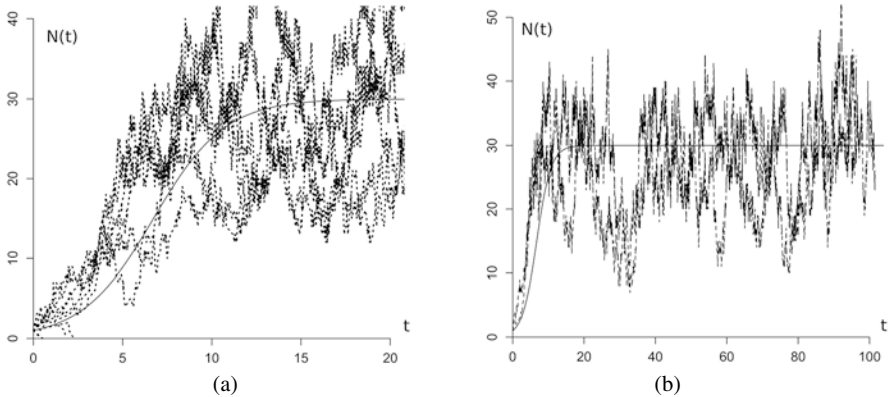


Fig. 4.3 Some simulations of a birth-and-death process $N(t)$ corresponding to the logistic differential equations: $\lambda_i = bi$, $\mu_i = (d + i(b - d)/K)i$. Here $b = 1$, $d = 0.5$, $K = 30$, $N(0) = 1$. (a) 10 simulations on a short interval: 4 of those undergo early extinction; (b) 2 of the simulations not going extinct on a longer time interval. In both cases, the solid line represents the solution of the differential equation $n'(t) = rn(t)(1 - n(t)/K)$ with $r = 0.5$, $K = 30$

tral limit theorems for the convergence of $N^{(K)}(t)$. These can be used to analyze the fluctuations around the equilibrium of the trajectories, but this is definitely beyond the level of this book.

Finally, as discussed above, all these realizations of the process will eventually reach 0, leading to population extinction, but this is very difficult to see on the time scale at which simulations are run.

Problems

4.1. Immigration-and-death processes

Let us consider a birth-and-death process in which the rate of transitions from m to $m + 1$ is α , $m \geq 0$; the rate of transitions from m to $m - 1$ is γm , $m \geq 1$.

1. Write down the Kolmogorov backward and forward equations for this model.
2. Noting that the model is considered in (4.9), compute its stationary probability distribution; is it one of the distributions that are considered in introductory courses in probability theory?

4.2. Immigration-birth-and-death

Let us consider a birth-and-death process in which the rate of transitions from m to $m + 1$ is $\beta(m + 1)$, $m \geq 0$; the rate of transitions from m to $m - 1$ is γm , $m \geq 1$.

1. Study under which conditions the process has a stationary probability distribution.
2. When it exists, compute it; is it one of the distributions that are considered in introductory courses in probability theory?
3. Intuitively, what happens when a stationary distribution does not exist?
4. Change the process, assuming that $\lambda_i = 0$ for $i \geq K$ while the other transitions are as above. Show that a stationary distribution always exists (if $\beta > 0$) and compute it.

4.3. Birth-and-death processes of logistic type

Assume

$$\lambda_0 = 0 \quad \text{and} \quad \lambda_i \leq \eta \mu_i \quad \text{for } i \text{ large enough with } \eta < 1.$$

Show that the probability of extinction is 1, starting from any initial population size $N(0)$.

4.4. Extinction time for logistic birth-and-death processes

Assume

$$\lambda_i = \beta i, \quad \mu_i = (\mu + \nu i)i$$

where all parameters are positive.

1. As it is known from Problem (4.3) that extinction is certain, write down the (infinite) system of linear equations for the expected times to extinction $W_i = \mathbb{E}(\tau | N(0) = i)$.

2. Discuss how the system could be approximated by truncating it to N equations, and how the number N could be chosen.
3. With the aid of a computer program for solving linear systems, choose $\mu = 1$, $\lambda = 1.2$ and for various values of ν , find what an appropriate value of N could be (one can increase N up to the point where W_0 does not change any more); compare the results obtained in this way with those obtained with model (4.23) (see Fig. 4.1).

4.5. Extinction time conditional on extinction

Consider the Malthusian model (4.2) with $\lambda > \mu$. We wish to find a system of equations for

$$W_i = \mathbb{E}(\tau | N(0) = i, \tau < \infty).$$

1. Using Bayes' rule, show that we can obtain the transition probabilities for the embedded jump chain conditional on extinction as follows

$$\mathbb{P}(Z_{n+1} = i+1 | Z_n = i, \tau < \infty) = \frac{\mathbb{P}(\tau < \infty | Z_{n+1} = i+1) \mathbb{P}(Z_{n+1} = i+1 | Z_n = i)}{\mathbb{P}(\tau < \infty | Z_n = i)},$$

$$\mathbb{P}(Z_{n+1} = i-1 | Z_n = i, \tau < \infty) = \frac{\mathbb{P}(\tau < \infty | Z_{n+1} = i-1) \mathbb{P}(Z_{n+1} = i-1 | Z_n = i)}{\mathbb{P}(\tau < \infty | Z_n = i)}.$$

2. Show that W_i solve system (4.19) exchanging λ and μ .
3. Interpret the result.

4.6. Sterile male release

The release of sterile males is a technique that sometimes has been applied in the attempt to eradicate pests. The idea is that a certain proportion of females will mate with the released sterile males and will not produce offspring, leading to a reduction of the population. Clearly, this can be effective only if sterile males are quite abundant compared to normal males.

Repeating this process for a few generations (while normal males become less and less abundant) could lead to a strong reduction of the population, and possibly to extinction.

We make extreme assumptions, in order to be able to build a very simplified model of this mechanism in the form of a birth-and-death process:

- assume that the number of females and 'normal' males is at all times equal: a male dies when and only when a female dies (at rate μ , independently of population size); offspring are born in pairs (one male and one female);
- assume that the number of sterile males is kept constant at the value S (as soon as one dies, it is replaced by a newly released one);
- assume that each female mates at rate λ (independently of population size) with a male chosen at random among the normal and sterile ones present in the population: if the male chosen is normal, it produces one female and one male; if it is sterile, it does not produce offspring.

1. Write the infinitesimal transition rates for this process (i.e., the rates at which the number of females changes from j to a different value).
 2. Write down the corresponding Kolmogorov differential equations.
 3. Noting that 0 is an absorbing state for the process, write down a system for the probabilities of the population to become extinct sooner or later, conditional on the initial number of females (and males) being equal to j . Intuitively, will these probabilities always be equal to 1?
 4. Modify the model by assuming that there exists a level $K > 0$, such that when the number of females reaches the number K the mating rate drops to 0, while being given by the model above for $j < K$. Noting that extinction is certain, write down a system of equation for the mean time to extinction, conditional on the number of females (and males) at time 0.
 5. Assume $K = 3$, $\lambda = 1.2$, $\mu = 1$. Find the value of T_1 , the mean time to extinction, conditional on 1 being the number of females (and males) at time 0.
-

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Spatial spread of a population

XXXVI

Fins possibles de l'âge d'or:

a) les âges d'argent

Il arrive donc un temps où le territoire occupé (et occupable) ne fournit plus la nourriture nécessaire au groupe devenu trop nombreux. Un premier ensemble de solutions se présente, celles qui diffèrent en quelque sorte la fin de l'âge d'or et qui laissent encore quelque espoir de voir continuer l'abondance sans travail. Ce sont la migration (massive et globale, quelques éléments pouvant rester cependant en arrière) vers un nouveau territoire; ...¹

Raymond Queneau, "Une histoire modèle", 1966

After age structure, considered in Sect. 2.5 of Chap. 2, another source of heterogeneity in a population is the fact that individuals are located at different positions in the geographical region occupied by the population. Thus the description of the spatial structure of the population may become important if the habitat is not spatially homogeneous. From the viewpoint of the mechanisms regulating the growth of a population in a spatially structured habitat, we need to model the vital rates as depending on the location and, more essentially, the mechanism regulating the movement of individuals.

The first considerable attempt to model spatial spread of a population is due to Skellam [5] whose models are still a valid tool to approach the problem of population dispersal. The basic idea is the mechanistic view that assimilate individuals to physical particles moving at random, as it is explicitly noticed by Skellam at the incipit of his paper:

the mathematical methods employed in the present treatment are largely the natural outcome of the solution of the well-known random-walk problem ...

Thus, equations regulating the spread of a population have a counterpart in Brownian motion, Fourier heat diffusion, Fickian diffusion, at least as far as we may con-

¹ Possible ends of the golden age: a) the silver age/ Thus a time comes when the occupied (and occupable) territory does not provide any more the resources necessary to the group, now too large. A first set of solutions are available, those that try to delay, in some way, the end of the golden age, and still give some hope to keep the abundance of resources without working. It is migration (massive and global, though some individual can be left behind) to a new territory ...

sider individuals moving at random. Other population models are based on directed motion; especially models of cell motion are often based on more complex mechanisms than simple diffusion. However, we will restrict ourselves to random diffusion as a starting point and a basic paradigm.

In the following section we will adopt a general framework based on the concept of *population flux* able to include different models by specifying its constitutive form. Then, in the other sections, we will analyze and discuss some basic models and problems such as existence of non homogeneous steady states and of traveling waves. The mathematical methods underlying our presentation in this chapter are somewhat classic. In particular we use extensively the method of separation of variables to solve and analyze the equations. These methods are part of the background a student in Mathematics is usually acquainted to, and we refer to basic text such as [6] for a tutorial itinerary through the subject.

5.1 A general framework

We consider a habitat displayed in a d -dimensional spatial region $\Omega \subset \mathbb{R}^d$, with $d \leq 3$. In this section, we take, for the sake of generality, $d = 3$ so that $\mathbf{x} \equiv (x, y, z)$ denoting position in Ω and $t \geq 0$ denoting time. Then the state of the population is represented through the scalar function

$$p(t, \mathbf{x}), \quad t \geq 0, \quad \mathbf{x} \in \Omega$$

i.e. with the *density* of the population with respect to space, at time t .

Namely, for any given region $V \subset \Omega$ we have that

$$P_V(t) = \int_V p(t, \mathbf{x}) dx dy dz$$

is the number of individuals in the region V at time t .

Population diffusion and growth are respectively regulated by the two terms:

- **$\mathbf{J}(t, \mathbf{x})$: population flux**, a vector field (dimensions $[N \times t^{-1} \times l^{-2}]$) such that

$$\mathbf{J}(t, \mathbf{x}) \cdot \mathbf{n}_\sigma(\mathbf{x}) d\sigma dt$$

gives the number of individuals crossing the infinitesimal surface $d\sigma$ at \mathbf{x} , in the time interval $[t, t + dt]$, in the direction of the normal $\mathbf{n}_\sigma(\mathbf{x})$ to $d\sigma$;

- **$f(t, \mathbf{x})$: total growth rate**, a term accounting for the vital (demographic) processes regulating population *growth* at \mathbf{x} ; it is a *density* rate with dimensions $[N \times t^{-1} \times l^{-3}]$ and it is often assumed to be *local* in the form

$$f(t, \mathbf{x}) = F(t, \mathbf{x}, p(t, \mathbf{x})) .$$

The general equation governing population changes is then obtained, in the same spirit of continuous mechanics, by imposing conservation of the number of individuals in any region V ; namely we have

$$\frac{d}{dt} \int_V p(t, \mathbf{x}) dx dy dz = - \int_{\partial V} \mathbf{J}(t, \mathbf{x}) \times \mathbf{n}_\sigma(\mathbf{x}) d\sigma + \int_V f(t, \mathbf{x}) dx dy dz$$

hence, transforming the surface integral into a volume integral, we have

$$\int_V (p_t(t, \mathbf{x}) + \nabla \mathbf{J}(t, \mathbf{x}) - f(t, \mathbf{x})) dx dy dz = 0 .$$

Since the region V is chosen arbitrarily in Ω , we then get

$$p_t(t, \mathbf{x}) = -\nabla \mathbf{J}(t, \mathbf{x}) + f(t, \mathbf{x}). \quad (5.1)$$

From this equation we can obtain different models putting together different mechanisms of diffusion and of population growth. The simplest constitutive form for the flux is suggested by an analogy with the *Fick law* and has the following form:

$$\mathbf{J}(t, \mathbf{x}) = -D \nabla p(t, \mathbf{x}) , \quad (5.2)$$

where we assume that the flux is proportional to the gradient of the population density and points to the opposite direction. This mechanism can be interpreted as the tendency of the population to move towards the *less crowded* part of the habitat. The constant D (*diffusion constant*) is a measure of the intensity of the displacement. With the constitutive form (5.2), if we disregard the vital dynamics of the population (i.e. the term $f(t, \mathbf{x})$), eq. (5.1) becomes the *heat equation*

$$p_t(t, \mathbf{x}) = D \Delta p(t, \mathbf{x}) , \quad (5.3)$$

describing both heat flow and particles diffusion.

In the same spirit of the previous formulation we may consider a more general constitutive equation for the flux:

$$\mathbf{J}(t, \mathbf{x}) = -D(\mathbf{x}) \nabla p(t, \mathbf{x}) + \mathbf{v}(\mathbf{x}) p(t, \mathbf{x}) ,$$

where we now let the diffusion constant $D(\mathbf{x})$ to depend on the position in the habitat and add an *advection term* $\mathbf{v}(\mathbf{x}) p(t, \mathbf{x})$ to take into account the possibility that at each place in the habitat the population may migrate for “local” reasons following a velocity field $\mathbf{v}(x)$.

Thus, a model for the description of a population, spreading in an region Ω , is the *reaction diffusion equation*

$$p_t(t, \mathbf{x}) = \nabla \cdot (D(\mathbf{x}) \nabla p(t, \mathbf{x}) - \mathbf{v}(\mathbf{x}) p(t, \mathbf{x})) + F(t, x, p(t, \mathbf{x})),$$

where we have included the term $F(t, x, p(t, \mathbf{x}))$ that has also to be specified according to the mechanism we believe as responsible of death and births in the population. For this term we may refer to the different growth mechanisms we have introduced in Chap. 1. In the simplest cases, we adopt one of the standard rates:

- **Malthus model:** $F(t, x, p(t, \mathbf{x})) = r p(t, \mathbf{x});$
- **Verhulst model:** $F(t, x, p(t, \mathbf{x})) = r \left(1 - \frac{p(t, \mathbf{x})}{K} \right) p(t, \mathbf{x}).$

Finally, the diffusion process must be implemented with *boundary conditions* specifying what happens at the border of the habitat. These actually lead to classical boundary conditions such as *Dirichlet's*:

$$P(t, \mathbf{x}) = 0, \quad t \geq 0 \quad \forall \mathbf{x} \in \partial \Omega$$

in the case of an *extremely inhospitable* border. Namely this is the case of an habitat surrounded by so harsh conditions that the population can't survive and its density vanishes already on the boundary.

Instead, for a *perfectly segregated habitat*, we impose *null-flux conditions* across the border $\partial \Omega$:

$$\mathbf{J}(t, \mathbf{x}) \times \mathbf{n}(\mathbf{x}) = -D(\mathbf{x}) \nabla p(t, \mathbf{x}) \times \mathbf{n}(\mathbf{x}) + \mathbf{v}(\mathbf{x}) p(t, \mathbf{x}) \times \mathbf{n}(\mathbf{x}) = 0, \quad \mathbf{x} \in \partial \Omega,$$

where $\mathbf{n}(\mathbf{x})$ is the outer normal to the boundary $\partial \Omega$ at the point \mathbf{x} .

Else, if we assume a kind of *immigration policy*, we can take:

$$\mathbf{J}(t, \mathbf{x}) \times \mathbf{n}(\mathbf{x}) = m(\mathbf{x}, p(t, \mathbf{x})) \quad \mathbf{x} \in \Omega,$$

where the function $m(\mathbf{x}, p(t, \mathbf{x}))$ specifies the policy, possibly depending on the population density.

5.2 The random-walk interpretation

The classical interpretation of the diffusion equation, as the macroscopic description of a microscopic process, is also applicable to populations. We focus on the 1-dimensional case, and consider an individual that at each time step Δt , steps to the right or to left of a basic length unit Δx , with equal probability (see Fig. 5.1). Thus, if $p(x, t)$ is interpreted as the probability distribution of this random walk process we have

$$p(x, t) = \frac{1}{2}p(x - \Delta x, t - \Delta t) + \frac{1}{2}p(x + \Delta x, t - \Delta t) \quad (5.4)$$

because position x can be reached at time t , in one step, both coming from $x - \Delta x$ and from $x + \Delta x$. Then, since

$$\begin{aligned} p(x \pm \Delta x, t - \Delta t) &= p(x, t) \pm p_x(x, t)\Delta x - p_t(x, t)\Delta t \\ &\quad + \frac{1}{2}(p_{xx}(x, t)(\Delta x)^2 \mp 2p_{xt}(x, t)\Delta x\Delta t + p_{tt}(x, t)(\Delta t)^2) \\ &\quad + O((\Delta x)^2 + (\Delta t)^2), \end{aligned}$$

substituting into (5.4), we have

$$\begin{aligned} p(x, t) &= p(x, t) - p_t(x, t)\Delta t + \frac{1}{2}p_{xx}(x, t)(\Delta x)^2 + \frac{1}{2}p_{tt}(x, t)(\Delta t)^2 \\ &\quad + O((\Delta x)^2 + (\Delta t)^2) \end{aligned}$$

so that

$$p_t(x, t) = \frac{1}{2}p_{xx}(x, t)\frac{(\Delta x)^2}{\Delta t} + \frac{1}{2}p_{tt}(x, t)\Delta t + \frac{1}{\Delta t}O((\Delta x)^2 + (\Delta t)^2).$$

Now, adopting the procedure typical of the *Brownian motion* theory, we let $\Delta x \rightarrow 0$, $\Delta t \rightarrow 0$ under the constraint

$$\frac{\Delta x^2}{\Delta t} = 2D, \quad (5.5)$$

where D is the *diffusion constant*. Thus, going to the limit with (5.5), we get

$$p_t(x, t) = Dp_{xx}.$$



Fig. 5.1 The random walk on a line. At time $t = 0$ the individual is placed at $x = 0$ and, after a time span Δt , he moves a step of length Δx , to the right or to the left with equal probability $p = 1/2$. Repeating the process n times, he reaches the point $x = m\Delta x$ at time $t = n\Delta t$

We remark that the constraint (5.5) implies that, in the continuous limit, individuals move with infinite velocity. This is a typical feature of random diffusion and it may be considered a limit of the model shared, however, with all the traditional models describing diffusion in the context of Physics.

5.3 Diffusion under Malthusian growth (Skellam model)

We now consider a population spreading in an one-dimensional habitat by *random diffusion with no drift* and undergoing Malthusian growth. We focus on the problem

$$\begin{cases} p_t(t, x) = Dp_{xx}(t, x) + rp(t, x) \\ p(0, x) = p_0(x) \end{cases} \quad (5.6)$$

on the population density $p(x, t)$. This equation, in the context of population dynamics is known as the *Skellam model* after J.G. Skellam [5] who first considered it in connection with population spread. The model depends on the two parameters r and D , previously defined as the Malthus parameter and the diffusion constant respectively. We assume $r > 0$ and scale (5.6) to dimensionless variables by the transformation²

$$t \rightarrow \tilde{t} = rt, \quad x \rightarrow \tilde{x} = \sqrt{\frac{r}{D}}x, \quad p \mapsto u = \frac{1}{N_0} \sqrt{\frac{D}{r}} p$$

with

$$N_0 = \int_{\Omega} p_0(x) dx.$$

Then, renaming \tilde{x} and \tilde{t} into x and t respectively, we have

$$\begin{cases} u_t(t, x) = u_{xx}(t, x) + u \\ u(0, x) = u_0(x) \end{cases} \quad (5.7)$$

where

$$u_0(x) = \frac{1}{N_0} \sqrt{\frac{D}{r}} p_0 \left(\sqrt{\frac{D}{r}} x \right) \quad \text{and} \quad \int_{\Omega} u_0(x) dx = 1.$$

We first consider the case of an infinite habitat $\Omega = (-\infty, +\infty)$ and suppose that at time $t = 0$ the population's size is N_0 and is concentrated at $x = 0$. Thus, denoting by $\delta(x)$ the Dirac distribution centered at $x = 0$, we have the initial condition

$$p(0, x) = N_0 \delta(x) \quad (5.8)$$

² Note that by (5.5) D has dimensions $[l^2 \times t^{-1}]$ and that $\xi = \sqrt{\frac{D}{r}}$ is a natural intrinsic unit for space.

and, correspondingly

$$u(0, x) = \delta(x) , \quad (5.9)$$

for the dimensionless variable. Then the solution of (5.7) is (see Problem 5.1)

$$u(t, x) = \frac{1}{2\sqrt{\pi t}} e^{\left(t - \frac{x^2}{4t}\right)}, \quad t > 0 \quad (5.10)$$

and we are able to draw some conclusions on the population spread relating the idealized model (5.6) to empirical observations of the habitat.

In fact since $u(t, x) > 0$ for any $t > 0$ and $x \in (-\infty, +\infty)$, we may say that the occupied habitat is infinite, corresponding to the assumption of infinite speed. However we can retrieve the concept of a finite growth of species range by assuming that each species living in a given habitat is observed only if its abundance is above a certain value. Thus we fix a threshold value p^* over which the species can be detected and look for the so-called *range* of the population, i.e. the area in which the species density $p(t, x)$ is above the threshold p^* . Actually this threshold is typical of the species: it is close to 0 for those species easy to detect and higher for those difficult to observe.

Corresponding to a threshold value p^* , and in view of the non-dimensional problem (5.7), we have the dimensionless threshold

$$u^* = \frac{p^*}{N_0} \sqrt{\frac{D}{r}}$$

and we compute the position $\Lambda(t)$ at which the population reaches the value u^* . So we have

$$u(t, \Lambda(t)) = u^*$$

and through the explicit form of the solution (5.10), we get

$$\Lambda(t) = \sqrt{4t^2 - 2t \ln \gamma t} \quad (5.11)$$

where

$$\gamma = 4\pi(u^*)^2 = \frac{4\pi D}{r} \left(\frac{p^*}{N_0}\right)^2.$$

Of course (5.11) is meaningful as far as $2t - \ln \gamma t > 0$. Indeed, for t small enough $\Lambda(t) > 0$, but it may vanish at those value of t such that the argument of the square root becomes negative. Thus we set

$$\Lambda(t) = 0 \quad \text{for} \quad 2t - \ln \gamma t < 0.$$

With this remark the graph of $\Lambda(t)$ is shown in Fig. 5.2, for different values of γ . We see that, for small values of γ , the range increases with time, while for high values of γ (see $\gamma = 7$ in Fig. 5.2) after a first phase during which the range decreases to zero, the population undergoes an *establishment phase* during which it is not observed. In all cases after the establishment, the range increases and the population spreads with

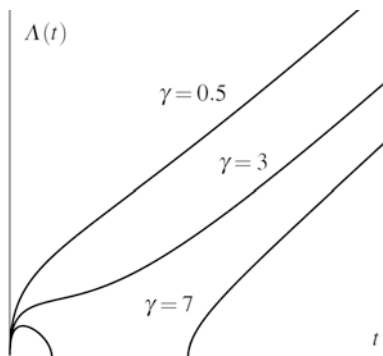


Fig. 5.2 The range of a population following Skellam model, for different values of the parameter γ . For $\gamma = 7$, the population enters the establishment phase before becoming detectable

a front $\Lambda(t)$ traveling at a rate $\frac{\Lambda(t)}{t}$ such that

$$\lim_{t \rightarrow +\infty} \frac{\Lambda(t)}{t} = 2.$$

Note that in the case described above we have assumed $r > 0$ so that the population grows and invades the habitat. The case of a negative Malthusian parameter is similar and is proposed as Problem 5.1. In this case the range after an initial phase shrinks and vanishes as the population goes extinct.

Finally note that, going back to the original dimensioned variables, the range is

$$L(t) = \sqrt{\frac{D}{r}} \Lambda(rt)$$

and

$$\lim_{t \rightarrow +\infty} \frac{L(t)}{t} = 2\sqrt{rD}.$$

We now consider the same problem (5.6) on a *limited habitat*, namely on the interval $[0, L]$, with different possible conditions at the boundary (the points $x = 0$ and $x = L$). Since we focus on the dimensionless form (5.7), the original interval is scaled to $[0, \Lambda]$ with

$$\Lambda = \sqrt{\frac{r}{D}} L.$$

Then we complete problem (5.7) with one of the two basic conditions:

- **Homogeneous Dirichlet conditions** (inhospitable border):

$$u(t, 0) = u(t, \Lambda) = 0;$$

- **No-flux Neumann conditions** (segregated habitat):

$$u_x(t, 0) = u_x(t, \Lambda) = 0.$$

By separation of variables we get the solution of (5.7) in the form of a Fourier series. Namely for the case of an inhospitable border we have

$$u_D(t, x) = e^t \sum_{n=1}^{\infty} c_n e^{-\frac{n^2 \pi^2}{\Lambda^2} t} \sin\left(\frac{n\pi}{\Lambda} x\right), \quad (5.12)$$

and, for the case of a segregated habitat

$$u_N(t, x) = e^t \sum_{n=0}^{\infty} c_n e^{-\frac{n^2 \pi^2}{\Lambda^2} t} \cos\left(\frac{n\pi}{\Lambda} x\right). \quad (5.13)$$

Here c_n are the Fourier coefficients, depending on the initial datum $u_0(x)$. Note that in both cases, the first coefficient (c_1 in the case of Dirichlet conditions, c_0 in the case of Neumann's) is positive because $u_0(x) \geq 0$ (and not trivial).

We examine these formulas in order to discuss the behavior of the solutions. In fact focusing on the Dirichlet condition case (5.12) we have

$$u_D(t, x) = e^{\left(1 - \frac{\pi^2}{\Lambda^2}\right)t} \left[c_1 \sin\left(\frac{\pi}{\Lambda} x\right) + O(t, x) \right]$$

with

$$O(t, x) = \sum_{n=2}^{\infty} c_n e^{-\frac{(n^2-1)\pi^2}{\Lambda^2} t} \sin\left(\frac{n\pi}{\Lambda} x\right).$$

Thus,

$$\lim_{t \rightarrow +\infty} O(t, x) = 0, \quad \text{uniformly in } [0, \Lambda],$$

and the solution behaves asymptotically as

$$u_D(t, x) \approx c_1 e^{\left(1 - \frac{\pi^2}{\Lambda^2}\right)t} \sin\left(\frac{\pi}{\Lambda} x\right). \quad (5.14)$$

Moreover, considering the total population in the habitat, we have

$$P_D(t) = \int_0^{\Lambda} u_D(t, x) dx \approx \frac{2\Lambda}{\pi} c_1 e^{\left(1 - \frac{\pi^2}{\Lambda^2}\right)t} \quad (5.15)$$

and, from this, we obtain the *asymptotic profile*

$$\omega_D(t, x) = \frac{u_D(t, x)}{P_D(t)} \approx \frac{\pi}{2\Lambda} \sin\left(\frac{\pi}{\Lambda} x\right)$$

i.e. the pattern emerging from an initial distribution as time goes on.

Formula (5.15) provides an insight to determine population survival or extinction. In fact, in order for the population to survive we have the condition

$$\Lambda^2 > \pi^2 \quad (5.16)$$

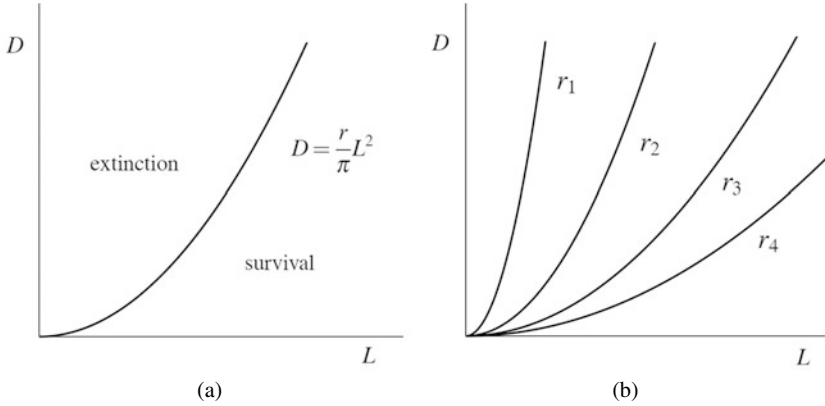


Fig. 5.3 Minimal length for survival. (a) the curve divides the plane into two regions for extinction and survival respectively. To each choice of the parameters D and r a minimal length L_{min} is determined; (b) different curves for different values of the growth rate r ; the minimal length decreases as r increases

that, in terms of the original dimension parameters, reads

$$\frac{r}{D} L^2 > \pi^2. \quad (5.17)$$

Thus we find the extinction-survival region, in the parameter space, shown in Fig. 5.3. We see that, for a given Malthusian parameter $r > 0$, diffusion and habitat size “play against each other”. In fact, we see that *large diffusion constants imply a larger habitat in order the population to survive*. In fact the faster the population diffuses, the earlier the border is reached and the faster the population exits the habitat failing colonizations.

Considering now the case of Neumann conditions, we have

$$u_N(t, x) = e^t [c_0 + O(t, x)]$$

again with

$$\lim_{t \rightarrow +\infty} O(t, x) = 0 \quad \text{uniformly in } [0, \Lambda].$$

Thus in this case we have the asymptotic form of the solutions as

$$u_N(t, x) \approx c_0 e^t$$

and for the total population and profile

$$P_N(t) \approx \Lambda c_0 e^t, \quad \omega_N(t, x) \approx \frac{1}{\Lambda}.$$

In this case we conclude saying that there are no habitat conditions for survival, because the population will *always survive* and from the spatial viewpoint the population tends to reach an homogeneous distribution (a constant profile). Thus, since

the population does not exit from the habitat, survival is granted and no pattern will arise because diffusion tends to homogenize the population abundance through the habitat.

5.4 The heterogeneous habitat

The previous models concern a homogeneous habitat, so that the diffusion constant D and the Malthusian parameter r are constant with respect to the space variable. A general model for a *heterogeneous habitat* is instead ruled by a diffusion equation with variable coefficients. We will be concerned with the one-dimensional case, namely with the equation

$$p_t(t, x) = (D(x)p_x(t, x))_x + r(x)p(t, x), \quad (5.18)$$

implemented with convenient boundary conditions at the ends of a given interval $[L_-, L_+]$ representing the region where the species lives.

Also in this case we can resort to separation of variables to obtain the solution in the form of a Fourier series

$$p(t, x) = \sum_{n=1}^{\infty} c_n e^{\lambda_n t} X_n(x) \quad (5.19)$$

where the sequence of eigenvalues λ_n and of the respective eigenfunctions $X_n(x)$ are provided by a Sturm-Liouville problem such as

$$\begin{cases} (D(x)X'(x))' + (r(x) - \lambda)X(x) = 0 \\ X'(L_-) = X'(L_+) = 0 \end{cases} \quad (5.20)$$

where we adopt no-flux boundary conditions, but also other conditions could be considered.

A general approach to such problems is presented in [2], where also the case of a multi-dimensional domain is treated. However, to our purposes, we may refer to the following fairly general result stating that the expansion (5.19) is possible:

consider problem (5.20) with

- $D(\cdot) \in C^{1+\alpha}([L_-, L_+])$, $D(x) > 0$ in $[L_-, L_+]$;
- $r(\cdot) \in L^\infty([L_-, L_+])$;

then there exist a sequence of eigenvalues λ_n such that

$$\lambda_1 > \lambda_2 \geq \lambda_3 \geq \dots \geq \lambda_k \geq \dots, \quad (5.21)$$

with the respective eigenfunctions $X_n(\cdot)$ providing a complete set for the Fourier expansion (5.19).

Indeed the main object we are interested in is the leading eigenvalue λ_1 that should be positive in order to have survival of the population. In fact, due to the above result we have the asymptotic expansion

$$p(t, x) = e^{\lambda_1 t} \left(c_1 X_1(x) + \sum_{n=2}^{\infty} c_n e^{(\lambda_n - \lambda_1)t} X_n(x) \right)$$

where

$$\lim_{t \rightarrow +\infty} \sum_{n=2}^{\infty} c_n e^{(\lambda_n - \lambda_1)t} X_n(x) = 0.$$

Thus the important question arises about how the leading eigenvalue depends upon the parameters of the problem; several results exist that determine this dependence in various cases [2].

Here we consider a special case that allows for explicit computations, where the habitat is split into two regions with different diffusion and growth rate. Namely we consider the interval $[-L, L]$ as an habitat and consider $D(x)$ and $r(x)$, piece-wise constant, defined as

$$D(x) = \begin{cases} D_1 & \forall x \in [-L, 0) \\ D_2 & \forall x \in [0, L]; \end{cases} \quad r(x) = \begin{cases} r_1 & \forall x \in [-L, 0) \\ r_2 & \forall x \in [0, L]. \end{cases}$$

We suppose that the population is confined in $[-L, L]$ so that we will adopt Neumann conditions at the border (i.e. at $x = -L$ and $x = L$). Moreover we assume that the left patch $[-L, 0]$ is favorable to population growth, taking $r_1 > 0$, while the right patch is supposed to be unfavorable with $r_2 < 0$. The question is:

under which conditions the population is able to survive, successfully exploiting the favorable patch, and compensate the negative life conditions of the unfavorable one.

We first rescale the problem adopting time and space units adapted to the left patch $[-L, 0]$. Namely we transform variables into the following ones:

$$t \rightarrow \tilde{t} = r_1 t, \quad x \rightarrow \tilde{x} = \sqrt{\frac{r_1}{D_1}} x, \quad p \rightarrow u = \frac{1}{N_0} \sqrt{\frac{D_1}{r_1}} p.$$

So that the problem transforms into

$$u_t(t, x) = (D(x)u_x)_x + r(x)u \quad (5.22)$$

with

$$D(x) = \begin{cases} 1 & \forall x \in [-\Lambda, 0) \\ d & \forall x \in [0, \Lambda]; \end{cases} \quad r(x) = \begin{cases} 1 & \forall x \in [-\Lambda, 0) \\ r & \forall x \in [0, \Lambda] \end{cases} \quad (5.23)$$

where

$$d = \frac{D_2}{D_1}, \quad r = \frac{r_2}{r_1}, \quad \Lambda = \sqrt{\frac{r_1}{D_1}}L.$$

Neumann conditions

$$u_x(t, -\Lambda) = u_x(t, \Lambda) = 0$$

complete the problem.

To solve the corresponding Sturm-Liouville problem (5.20), we split the problem into two parts

$$\begin{cases} X''_- + (1 - \lambda)X_- = 0 \\ X'_-(-\Lambda) = 0 \end{cases} \quad (5.24)$$

$$\begin{cases} dX''_+ + (r - \lambda)X_+ = 0 \\ X'_+(\Lambda) = 0 \end{cases} \quad (5.25)$$

and impose continuous differentiability at $x = 0$

$$X_-(0^-) = X_+(0^+), \quad X'_-(0^-) = X'_+(0^+). \quad (5.26)$$

Solving (5.24) we have for $x \in [-\Lambda, 0]$, we have

$$\begin{cases} X_-(x) = \cosh\left(\sqrt{\lambda - 1}(x + \Lambda)\right) & \text{for } \lambda > 1 \\ X_-(x) = 1 & \text{for } \lambda = 1 \\ X_-(x) = \cos\left(\sqrt{1 - \lambda}(x + \Lambda)\right) & \text{for } \lambda < 1 \end{cases} \quad (5.27)$$

and, solving (5.25) for $x \in [0, \Lambda]$

$$\begin{cases} X_+(x) = \cosh\left(\sqrt{\frac{\lambda - r}{d}}(x - \Lambda)\right) & \text{for } \lambda > r \\ X_+(x) = 1 & \text{for } \lambda = r \\ X_+(x) = \cos\left(\sqrt{\frac{r - \lambda}{d}}(x - \Lambda)\right) & \text{for } \lambda < r. \end{cases} \quad (5.28)$$

To match solutions at $x = 0$ we have to consider different cases according to the values of λ . Since $r < 0$ we focus on those cases corresponding to $\lambda \in (0, +\infty)$, because we are interested in finding possible positive eigenvalues. First we consider the case $\lambda \geq 1 > r$ corresponding to the first two options in (5.27) and to the top one in (5.28). Indeed we show that in this interval there is no eigenvalue. In fact, imposing (5.26) we have

$$\cosh\left(\Lambda\sqrt{\lambda - 1}\right) = A \cosh\left(\Lambda\sqrt{\frac{\lambda - r}{d}}\right)$$

and

$$(\sqrt{\lambda-1}) \sinh(\Lambda \sqrt{\lambda-1}) = A \left(\sqrt{\frac{\lambda-r}{d}} \right) \sinh \left(\sqrt{\Lambda \frac{\lambda-r}{d}} \right)$$

hence

$$(\sqrt{\lambda-1}) \tanh(\Lambda \sqrt{\lambda-1}) = \left(\sqrt{\frac{\lambda-r}{d}} \right) \tanh \left(\sqrt{\Lambda \frac{\lambda-r}{d}} \right)$$

which is impossible because the function $f(x) = x \tanh x$ is increasing.

We now consider the case $\lambda \in (0, 1)$. Actually we need to consider the bottom option in (5.27) and the top one in (5.28) getting

$$\cos(\Lambda \sqrt{1-\lambda}) = A \cosh \left(\Lambda \sqrt{\frac{\lambda-r}{d}} \right)$$

and

$$\sqrt{1-\lambda} \sin(\Lambda \sqrt{1-\lambda}) = A \sqrt{\frac{\lambda-r}{d}} \cosh \left(\Lambda \sqrt{\frac{\lambda-r}{d}} \right),$$

yielding the characteristic equation

$$\sqrt{1-\lambda} \tan(\Lambda \sqrt{1-\lambda}) = \sqrt{\frac{\lambda-r}{d}} \tanh \left(\Lambda \sqrt{\frac{\lambda-r}{d}} \right) \quad (5.29)$$

for $\lambda \in (0, 1)$.

To analyze (5.29) we consider the two functions

$$f(\lambda) = \sqrt{1-\lambda} \tan(\Lambda \sqrt{1-\lambda})$$

and

$$g(\lambda) = \sqrt{\frac{\lambda-r}{d}} \tanh \left(\Lambda \sqrt{\frac{\lambda-r}{d}} \right)$$

and look for intersections of their graph in the interval $\lambda \in (0, 1)$. The function $g(\lambda)$ is increasing and positive while the function $f(\lambda)$ is decreasing, vanishes at $\lambda = 1$ and has a vertical asymptote at

$$\lambda^* = 1 - \frac{\pi^2}{4\Lambda^2}.$$

In Fig. 5.4 these graphs are drawn in the two cases $\lambda^* > 0$ and $\lambda^* < 0$. In the first case we always have an intersection, in the second one an intersection occurs if and only if $f(0) > g(0)$ yielding the condition

$$\tan(\Lambda) > \sqrt{\frac{-r}{d}} \tanh \left(\Lambda \sqrt{\frac{-r}{d}} \right).$$

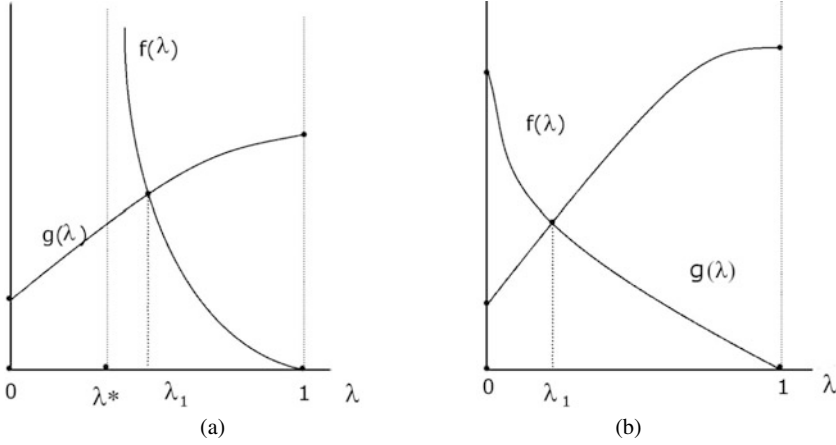


Fig. 5.4 Existence of a positive (leading) eigenvalue. (a) $\lambda^* > 0$, the graphs cross at least at $\lambda_1 > 0$; (b) $\lambda^* < 0$, the graphs cross if and only if $f(0) > g(0)$

Summarizing the above results, interpreting conditions in terms of the original parameters, we have:

a population living segregated in a two patch habitat, with patch 1 favorable to survival and patch 2 unfavorable, will survive if

$$L^2 > \frac{\pi^2 D_1}{4r_1}; \quad (5.30)$$

if (5.30) is not satisfied then the population will survive if

$$\sqrt{\frac{r_1}{D_1}} \tan \left(L \sqrt{\frac{r_1}{D_1}} \right) > \sqrt{\frac{-r_2}{D_2}} \tanh \left(L \sqrt{\frac{-r_2}{D_2}} \right). \quad (5.31)$$

We note that condition (5.30) is the same conditions (5.17) applied to the whole region $[-L, L]$ when survival is possible, provided the habitat is large enough to avoid fatal absorption at $x = L$. In the present case absorption is distributed through the non favorable path.

If condition (5.30) is not satisfied, condition (5.31) shows that survival is still possible if $-r_2/D_2$ is sufficiently small, i.e. diffusion in patch 2 is large enough and/or the extinction rate $-\rho_2$ is sufficiently small.

One can repeat similar computations for other cases (see Problem 5.3). In particular, it is instructive considering two regions of different size (L_1 and L_2) with the same diffusion coefficients D but differing in growth rate; the interesting case is when they differ in sign: say $r_1 > 0 > r_2$. From the analysis, we can obtain the following conclusion regarding the leading eigenvalue λ^* :

- in the limit as D goes to 0, $\lambda^* > 0$, however small is L_1 ;
- in the limit as D grows to ∞ , $\lambda^* > 0$ if and only if $r_1 L_1 + r_2 L_2 > 0$.

This principle can be generalized (see [1]) to any spatially varying growth rate $r(x)$:

- if $r(x) > 0$ in a set of positive measure, then in the limit as D goes to 0, $\lambda^* > 0$;
- in the limit as D grows to ∞ , $\lambda^* > 0$ if and only if $\int_{\Omega} r(x) dx > 0$.

The principle is quite intuitive: if there is very little diffusion, for the population to persist it is enough that the growth rate is positive somewhere; in this case the population will grow in that region, and the growth will not be overwhelmed by diffusion. On the other hand, if diffusion is very large, the system loses any spatial differentiation, and only average growth rate matters.

5.5 Diffusion under logistic growth

In Sect. 5.1 we have seen how reaction diffusion equations arise by coupling random diffusion with non-linear growth. Here we consider the special case of Verhulst growth as a prototype, providing the basic methods to be used in other models including for instance Allee effect or generalist predation. We consider the equation

$$p_t(t, x) = D p_{xx}(t, x) + r \left(1 - \frac{p(t, x)}{K} \right) p(t, x),$$

that we will study in connection with different boundary conditions.

A natural scaling of the variables

$$\tilde{t} = rt \quad \tilde{x} = \sqrt{\frac{r}{D}} x \quad \tilde{u} = \frac{u}{K}$$

leads to the dimensionless equation

$$u_t = u_{xx} + u(1 - u). \quad (5.32)$$

Equation (5.32) is known as the *Fisher equation* because it was originally considered by Fisher [4] to model diffusion of gene-frequency.

We look for steady states of (5.32), on some interval $[0, L]$, with boundary conditions to be specified afterwards. Namely we look for solutions that are constant with respect to time

$$u(t, x) = U(x)$$

and satisfy

$$U''(x) + U(x)(1 - U(x)) = 0. \quad (5.33)$$

Among steady states special cases are those of *homogeneous solutions*, i.e. solution that are also independent of the space variable, thus satisfying

$$U(x) = u^*, \quad u^*(1 - u^*) = 0.$$

For (5.33) we have the homogeneous solutions

$$U(x) = 0 \quad \text{and} \quad U(x) = 1, \quad (5.34)$$

however we should note that boundary conditions also enter in defining such solution so that, if we consider Dirichlet conditions at the end-points of some given interval, then we have only $U(x) = 0$, while with Neumann conditions we also have $U(x) = 1$.

We now focus on eq. (5.33) to discuss existence of *non-homogeneous solutions* in correspondence of the different boundary conditions. We note that (5.33) can be transformed into the first order system

$$\begin{cases} U'(x) = V(x) \\ V'(x) = U(x)(U(x) - 1) \end{cases} \quad (5.35)$$

and has a unique (local) solution when we impose an initial condition such as

$$U(0) = U_0, \quad V(0) = V_0. \quad (5.36)$$

We need to discuss this family of solutions in order to find a non-negative solution satisfying the boundary conditions we have on the problem. Now, multiplying both sides of (5.33) by $U'(x) = V(x)$ we get

$$\frac{d}{dx} (V^2(x) + G(U(x))) = 0$$

where

$$G(z) = 2 \int_0^z s(1 - s)ds = z^2 - \frac{2}{3}z^3. \quad (5.37)$$

Thus, solutions of (5.35) necessarily satisfies

$$V^2(x) + G(U(x)) = C \quad (5.38)$$

where C is a constant that for a solution satisfying (5.36) would be

$$C = V_0^2 + G(U_0). \quad (5.39)$$

Trajectories in the phase plane (U, V) are plotted in Fig. 5.5 that help to understand the nature of the solutions in view of the construction of solutions on a finite interval $[0, \Lambda]$, satisfying boundary conditions of Dirichlet or Neumann type.

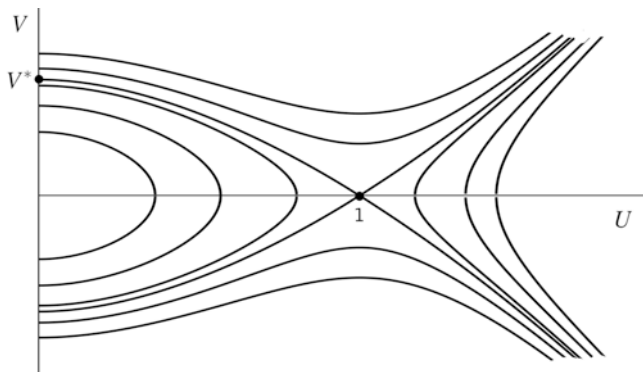


Fig. 5.5 Trajectories for system (5.35) in the phase plane (U, V) , based on the first integral (5.38). Trajectories starting and ending on the U axis correspond to solutions satisfying Dirichlet conditions. No solutions joining points on the V axis (Neumann conditions) are allowed

We soon note that Neumann conditions do not allow for non homogeneous solutions: in fact, in the phase plane (U, V) we see that no trajectory connects two points on the positive U semi-axis while, for a solution satisfying Neumann conditions, we should be able to obtain

$$V(0) = V(\Lambda) = 0 .$$

For imposing Dirichlet conditions, we look for a solution of (5.33) satisfying

$$U(0) = U(\Lambda) = 0 . \quad (5.40)$$

To this purpose, we first look for a solution $\bar{U}(x)$ on the half interval $[0, \Lambda/2]$ satisfying

$$\bar{U}(0) = 0, \quad \bar{U}\left(\frac{\Lambda}{2}\right) = u_m, \quad \bar{U}'\left(\frac{\Lambda}{2}\right) = 0 . \quad (5.41)$$

Then we set (see Fig. 5.6)

$$U(x) = \begin{cases} \bar{U}(x) & x \in [0, \Lambda/2] \\ \bar{U}(\Lambda - x) & x \in [\Lambda/2, \Lambda] \end{cases} . \quad (5.42)$$

Indeed, from the picture in the phase plane shown in Fig. 5.5, we see that such solutions $\bar{U}(x)$ correspond to the bounded trajectories lying in the positive quadrant, on the left of $U = 1$. Thus we should take $u_m < 1$ and look for the corresponding Λ satisfying $\bar{U}(\Lambda/2) = u_m$.

Now, since the solution $\bar{U}(x)$ must correspond to $C = G(u_m)$, it satisfies

$$\bar{U}'(x) = \sqrt{G(u_m) - G(\bar{U}(x))}, \quad \text{with} \quad \bar{U}(0) = 0 .$$

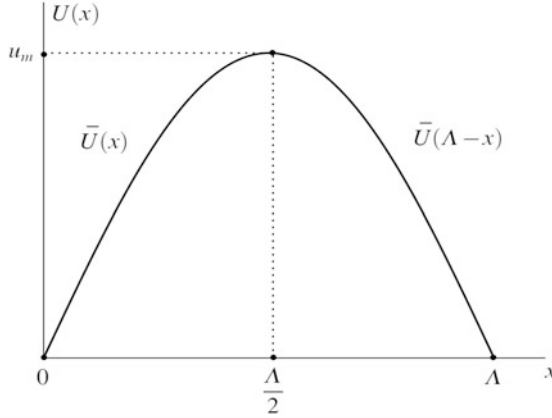


Fig. 5.6 The construction of a non-homogeneous steady state through (5.42). For each $\Lambda > \pi$ there exist one and only one $u_m < 1$ for such a solution to exist

Thus, solving this problem by separation of variables, $\bar{U}(x)$ is implicitly defined by

$$\int_0^{\bar{U}(x)} \frac{dz}{\sqrt{G(u_m) - G(z)}} = x. \quad (5.43)$$

Imposing the second condition in (5.41) we obtain the value of Λ as a function of $u_m \in [0, 1)$

$$\Lambda(u_m) = 2 \int_0^{u_m} \frac{dz}{\sqrt{G(u_m) - G(z)}}$$

and, changing variables in the integral, after some algebra we get

$$\Lambda(u_m) = 2 \int_0^1 \frac{d\sigma}{\sqrt{(1-\sigma) \left(1 + \sigma - \frac{2}{3}u_m(1 + \sigma + \sigma^2)\right)}}.$$

It is easy to see that $\Lambda(\cdot)$ is increasing and

$$\Lambda(0) = 2 \int_0^1 \frac{d\sigma}{\sqrt{(1-\sigma^2)}} = \pi, \quad \lim_{u_m \rightarrow 1} \Lambda(u_m) = +\infty,$$

as it is shown in Fig. 5.7. We have thus seen that for each $u_m < 1$, we can find $\Lambda > \pi$ such that $\bar{U}(\lambda/2) = u_m$. Note that that $\Lambda(0) = \pi$ is the minimum size for the habitat in order that a non-homogeneous steady state is feasible.

In conclusion we have:

for the Fisher equation (5.32) with Dirichlet boundary conditions, a unique non-homogeneous steady state exists if and only if $\Lambda > \pi$.

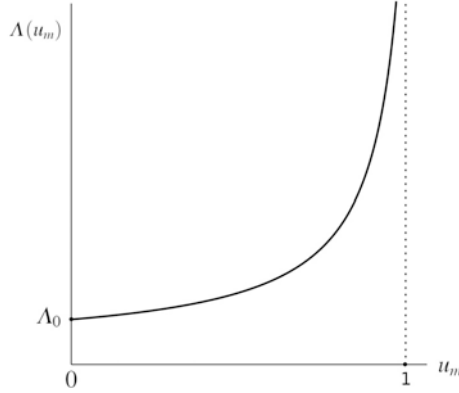


Fig. 5.7 The graph of Λ as a function of u_m . $\Lambda(0) = \pi$ and Λ is increasing with u_m , so that there is one and only one solution for $\Lambda > \pi$

In terms of the parameters of the model we have again condition (5.17), valid for the Skellam model.

As far as the stability of these steady states is concerned, we resort on linearization. Namely at a given steady state $U(x)$ we consider the equation

$$w_t(t, x) = w_{xx}(t, x) + F'(U(x))w(t, x), \quad (5.44)$$

on the deviation

$$w(t, x) = u(t, x) - U(x), \quad (5.45)$$

and look for the expansion

$$w(t, x) = \sum_{n=0}^{\infty} c_n e^{\lambda_n t} X_n(x), \quad (5.46)$$

where the functions X_n are determined by the boundary conditions. Thus we have asymptotic stability if

$$\lambda_n < 0 \quad \text{for all } n. \quad (5.47)$$

For the Fisher equation, if we consider the case of the *homogeneous solutions* (5.34), then (5.44) becomes

$$w_t = w_{xx} + F'(u^*)w, \quad x \in [0, \Lambda] \quad (5.48)$$

and the eigenvalues are

$$\lambda_n = F'(u^*) - \frac{n^2 \pi^2}{\Lambda^2} \quad (5.49)$$

with $n = 0, 1, 2, \dots$ in the case of Neumann conditions and $n = 1, 2, \dots$ in the case of Dirichlet's. Thus, since $F'(1) = -1$, the steady state $U(x) = 1$, with Neumann conditions, is asymptotically stable. Since $F'(0) = 1$, the steady state $U(x) = 0$, is unstable with Neumann conditions while, with Dirichlet conditions is stable if

$$\Lambda < \pi. \quad (5.50)$$

Finally we note that, in the case of Dirichlet conditions, when (5.50) is violated and the $U(x) = 0$ solution is unstable, the non-homogeneous solution (5.42) exists and inherits its stability.

Actually it is possible to prove that the non-homogeneous solution is a global attractor when it exists; similarly one can prove that, with Neumann boundary conditions, the homogeneous solution $u(t, x) \equiv 1$ is a global attractor. However, the proof of these results go beyond the scope of this book and we refer to [2] for a complete treatment of Fisher equation. Summarizing we have:

- with Neumann conditions $u_x(t, 0) = u_x(t, \Lambda) = 0$, Fisher equation (5.32) has only the homogeneous steady states $U(x) = 0$ and $U(x) = 1$; $U(x) = 0$ is unstable, while $U(x) = 1$ is a global attractor;
- with Dirichlet conditions $u(t, 0) = u(t, L) = 0$, Fisher equation (5.32) has the unique homogeneous steady state $U(x) = 0$, which is a global attractor for $\Lambda < \pi$, while for $\Lambda > \pi$ it is unstable and a unique non homogeneous steady state exists which is a global attractor.

5.6 Traveling waves

We consider now the single reaction-diffusion equation

$$u_t = u_{xx} + F(u) \quad (5.51)$$

on the infinite line, and look for solutions in the form

$$u(x, t) = \phi(x - ct) \quad x \in (-\infty, +\infty) \quad t \geq 0 \quad (5.52)$$

i.e. in the form of traveling waves. In fact (5.52) represents a function translating as t varies, at a speed c , to the right for $c > 0$ and to the left for $c < 0$. In (5.52) we have to find both the profile $\phi(\xi)$ and the traveling velocity c . We note that if the couple $(\phi(\xi), c)$ corresponds to a solution in the form (5.52), then the couple

$$\tilde{\phi}(\xi) = \phi(-\xi) \quad \tilde{c} = -c \quad (5.53)$$

corresponds to another solution, precisely to the solution with a profile symmetrical to the previous one, with respect to the vertical axis, and traveling to the opposite direction. Thus we will focus only on solutions with $c > 0$. In principle, we can have two types of waves (see Fig. 5.8):

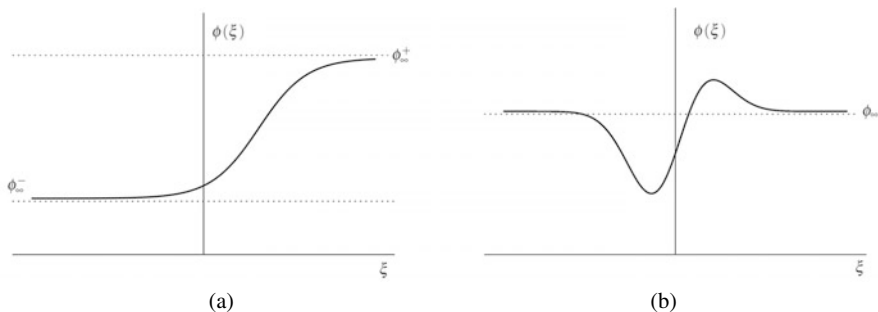


Fig. 5.8 Two different types of traveling waves: (a) the wave front such that $\phi(-\infty) = \phi_{\infty}^-$, $\phi(+\infty) = \phi_{\infty}^+$; (b) the wave pulse with $\phi(-\infty) = \phi(+\infty) = \phi_{\infty}$.

- **wave front**

a traveling wave such that the profile ϕ approaches different limits at $x = \pm\infty$, namely

$$\phi(-\infty) = \phi_{\infty}^-, \quad \phi(+\infty) = \phi_{\infty}^+ \quad (5.54)$$

with $\phi_{\infty}^- \neq \phi_{\infty}^+$;

- **pulse wave**

a traveling wave such that the profile ϕ approaches the same limits at $\pm\infty$:

$$\phi(-\infty) = \phi(+\infty) = \phi_{\infty}. \quad (5.55)$$

Now, in order that (5.52) satisfies (5.51), the profile $\phi(\xi)$ must satisfy:

$$\phi''(\xi) + c\phi'(\xi) + F(\phi(\xi)) = 0 \quad (5.56)$$

which is equivalent to the first order system

$$\begin{cases} \phi' = w \\ w' = -cw - F(\phi), \end{cases} \quad (5.57)$$

where we have introduced the auxiliary variable $w = \phi'$.

Note that, if we look for a solution $u(x, t)$ such that $u_x(x, t)$ converges as $x \rightarrow \pm\infty$, then together with (5.54) or (5.55) we also have

$$w(\pm\infty) = \phi'(\pm\infty) = 0 \quad (5.58)$$

and $(\phi_{\infty}^{\pm}, 0)$, $(\phi_{\infty}, 0)$ must be steady state of the system (5.57). In particular, $\phi_{\infty}^{\pm}, \phi_{\infty}$ must be zeros of $F(z)$, namely homogeneous steady state of (5.51).

We will first focus on the Fisher equation (5.32), then

$$F(\phi) = \phi(1 - \phi)$$

and we have only the two zeros $\phi_0 = 0$ and $\phi_1 = 1$. In the phase-plane (ϕ, w) we have that $(0, 0)$ and $(1, 0)$ are steady states of the system (5.57) and the sought profile ϕ must be the first component of a trajectory $(\phi(\xi), w(\xi))$ connecting such points.

It is important to know the nature of these points, thus we consider the Jacobians of (5.57)

$$J(0,0) = \begin{pmatrix} 0 & 1 \\ -1 & -c \end{pmatrix}, \quad J(1,0) = \begin{pmatrix} 0 & 1 \\ 1 & -c \end{pmatrix}.$$

Now, for $(0,0)$ we have the eigenvalues

$$\lambda^{\pm} = \frac{-c \pm \sqrt{c^2 - 4}}{2}; \quad (5.59)$$

then, since $c > 0$, $(0,0)$ is a stable point. Instead, $(1,0)$ turns out to be a saddle point (the eigenvalues are always one positive and one negative).

Now, since in the context of populations we look for ϕ non-negative, we have to exclude the case in which the eigenvalues at $(0,0)$ are complex. In fact, otherwise, the point $(0,0)$ would be a focus and ϕ would assume negative values. This remark yields the condition

$$c \geq 2 \quad (5.60)$$

which is necessary for existence of non-negative traveling solutions. The situation is shown in Fig. 5.9. In particular, from this figure we see that a wave front $\phi(\xi)$, connecting the two homogeneous states $u_1 = 1$ and $u_0 = 0$ is possible and, since $c > 0$, it proceeds from a high density zone to the low density one (see Fig. 5.10).

To prove that this is indeed the case, we consider Fig. 5.11 where the phase-plane is plotted with arrows representing the vector field of the system (5.57). In the picture, the line $w = -m\phi$ is also shown, with a normal $\mathbf{n} = (m, 1)$ pointing to the interior of the triangle ABC , i.e. $m > 0$. Now, the field on this line is

$$\mathbf{v} = (-m\phi, mc\phi - \phi(1 - \phi))$$

and the scalar product

$$\mathbf{v} \cdot \mathbf{n} = -m^2\phi + mc\phi - \phi(1 - \phi) = (-m^2 + mc - 1)\phi + \phi^2$$

is positive at any point of the segment AB if

$$m^2 - cm + 1 < 0$$

thus, if we choose

$$0 < \frac{c - \sqrt{c^2 - 4}}{2} < m < \frac{c + \sqrt{c^2 - 4}}{2}$$

the triangle ABC is invariant.

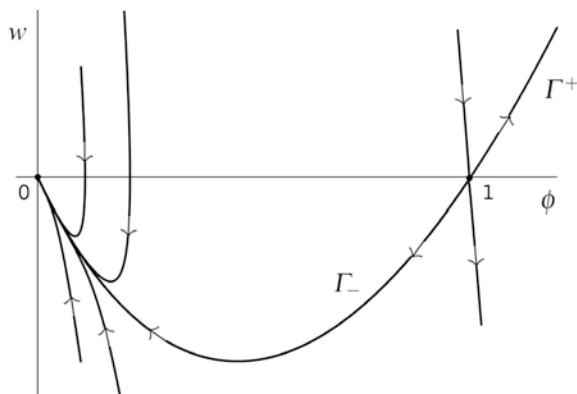


Fig. 5.9 Phase plane (ϕ, w) for system (5.51) with $c \geq 2$. The point $(0,0)$ is a stable node while $(1,0)$ is a saddle point. The curves Γ_+ and Γ_- are the unstable manifold of $(1,0)$ and Γ_- connects $(1,0)$ with $(0,0)$, providing the profile $\phi(\xi)$

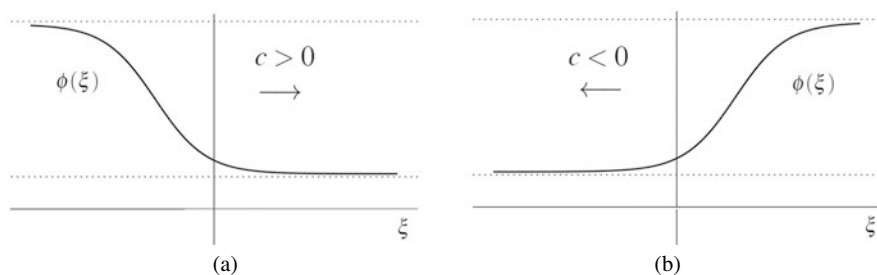


Fig. 5.10 Wave fronts in the two cases $c \geq 2$ (a) and $c \leq -2$ (b). Case (b) is obtained from case (a) through (5.53)

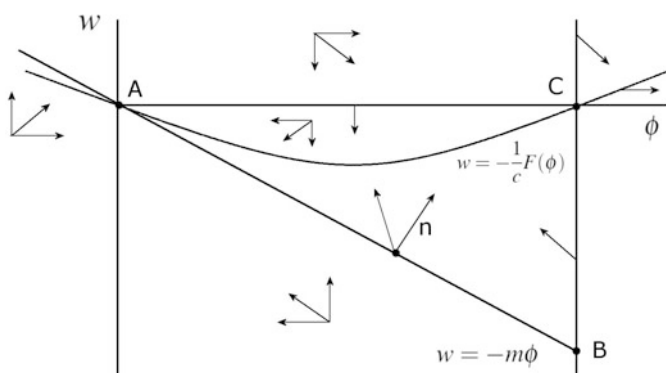


Fig. 5.11 The phase-plane for system (5.57) in the case of the Fisher equation. The picture of the two isoclines $w = 0$ and $w = -\frac{1}{c}F(\phi)$, together with the orientation of the differential field, help to prove that the trajectory Γ_- joins the two points $(0,0)$ and $(1,0)$

Now, of the two trajectories Γ_- and Γ_+ (see Fig. 5.9), only Γ_- enters the invariant triangle ABC and consequently it has to converge to the stable node $(0,0)$. As for Γ_+ , it lies to the right of the vertical line through the steady state $(1,0)$ and also in the positive quadrant, thus it cannot reach the origin. It is also clear that no pulse is compatible with the vector field and, in conclusion, we have the following statement:

for any $c \geq 2$ the Fisher equation has one unique traveling front with speed c .

Apart from the specific case of Fisher equation, we point out a general relationship between c and a possible wave front, useful to determine the sign of c . From (5.56), in fact we have

$$\frac{1}{2} \frac{d}{d\xi} (\phi'(\xi))^2 + c(\phi'(\xi))^2 + F(\phi(\xi))\phi'(\xi) = 0$$

and integrating (note that $\phi'(-\infty) = \phi'(+\infty) = 0$)

$$c \int_{-\infty}^{+\infty} (\phi'(\xi))^2 d\xi = - \int_{-\infty}^{+\infty} F(\phi(\xi))\phi'(\xi) d\xi.$$

Then, we have

$$c = - \frac{1}{\int_{-\infty}^{+\infty} (\phi'(\xi))^2 d\xi} \int_{\phi(-\infty)}^{\phi(+\infty)} F(s) ds. \quad (5.61)$$

In the specific case of the Fisher equation we have

$$\int_0^1 F(s) ds = \frac{1}{6} > 0,$$

so that we have

- $c > 0$ if $\phi(-\infty) = 1$ $\phi(+\infty) = 0$;
- $c < 0$ if $\phi(-\infty) = 0$ $\phi(+\infty) = 1$,

as we have already found.

Another interesting example of wave-fronts is the strong Allee-logistic model with diffusion (see (1.25))

$$u_t = Dp_{xx}(t,x) + r \left(1 - \frac{p(t,x)}{K} \right) \left(\frac{p(t,x)}{T} - 1 \right) p(t,x)$$

that can be conveniently rescaled into

$$u_t = u_{xx} + u(1-u)(\alpha u - 1) \quad (5.62)$$

where $\alpha = \frac{K}{T} > 1$ (in fact $K > T$).

The resulting framework for the search of the traveling front is now more complicated. In fact, in the case of eq. (5.62), the reaction term

$$F(u) = u(1-u)(\alpha u - 1) \quad (5.63)$$

has the three zeros

$$u_0 = 0, \quad u_1 = \frac{1}{\alpha}, \quad u_2 = 1$$

and system (5.57) has the steady states

$$A = (0, 0), \quad B = \left(\frac{1}{\alpha}, 0\right), \quad C = (1, 0).$$

However, in this particular case the wave-fronts can be computed explicitly just looking at a specific form of a trajectory for system (5.57). We consider, for instance, the case of a trajectory connecting the points $A = (0, 0)$ and $C = (1, 0)$, searching for it in the form of a parabola

$$w = A\phi(1 - \phi), \quad (5.64)$$

where the constant A has to be determined.

Now, because of (5.64), a trajectory $(\phi(\xi), w(\xi))$ must satisfy

$$w' = A(1 - 2\phi)\phi' = A(1 - 2\phi)w = A^2(1 - 2\phi)\phi(1 - \phi),$$

and, since $w' = -cw + F(\phi)$ (see (5.57)), we have

$$A^2(1 - 2\phi)\phi(1 - \phi) = -cA\phi(1 - \phi) - \phi(1 - \phi)(\alpha\phi - 1),$$

i.e., dividing by $\phi(1 - \phi)$,

$$(2A^2 - \alpha)\phi + 1 - cA - A^2 = 0.$$

As the previous identity has to hold for all ϕ , this gives

$$A_{\pm} = \pm\sqrt{\frac{\alpha}{2}}, \quad c_{\pm} = \pm\frac{2 - \alpha}{\sqrt{2\alpha}}$$

and to find ϕ we solve

$$\phi'_{\pm}(\xi) = w = \pm\sqrt{\frac{\alpha}{2}}\phi(1 - \phi),$$

from which we obtain the sought $\phi(\xi)$

$$\phi_{\pm}(\xi) = \frac{1}{1 + ke^{\mp\sqrt{\frac{\alpha}{2}}\xi}}, \quad (5.65)$$

where $k > 0$ is an arbitrary constant, since the profile is determined but for a translation. Note that the sign of c_{\pm} depends on α , namely if $\alpha > 2$ then $c_+ < 0$ ($c_- > 0$), if instead $\alpha < 2$ then $c_+ > 0$ ($c_- < 0$). Actually this is expected from (5.61) applied

to (5.63)

$$\int_0^1 F(\sigma) d\sigma = \frac{\alpha - 2}{12}.$$

In this case, differently from Fisher equation, we have found only the profiles (5.65), with the respective values for the speed. It can be shown that these are indeed the unique traveling wave connecting $u_0 = 0$ and $u_1 = 1$, namely we have (see [1] for a proof):

for the strong Allee-logistic equation (5.62), with $\alpha > 2$, there is a unique speed $c > 0$ such that there exists a wave front going from $u_1 = 1$ to $u_0 = 0$.

Of course, together with this profile we have the corresponding wave-front (5.53). The case $\alpha < 2$ is analogous.

Traveling solutions such as those that we have find in this section, play a particular role in the dynamics of the solutions of non linear problems on the infinite line. In fact such solutions are asymptotically attractive for solutions with initial data satisfying particular conditions.

In the case of Equation (5.62) the unique solution (5.65) we have found, is in fact the asymptotic limit of any solution starting from an initial datum satisfying particular bounds depending on α . Namely we have the typical result (see for instance [1]):

consider eq. (5.62) with $\alpha > 2$ endowed with the initial condition

$$u(0, x) = u_0(x)$$

satisfying

$$\liminf_{x \rightarrow -\infty} u_0(x) > \frac{1}{\alpha}, \quad \limsup_{x \rightarrow +\infty} u_0(x) < \frac{1}{\alpha}. \quad (5.66)$$

Then there exist constants $M > 0, \omega > 0, k > 0$ such that

$$|u(t, x) - \phi(x - ct)| \leq M e^{-\omega t}$$

with

$$\phi(\xi) = \frac{1}{1 + k e^{\sqrt{\frac{\alpha}{2}} \xi}}, \quad c = \frac{\alpha - 2}{\sqrt{2\alpha}}.$$

Note that with condition (5.66), the initial datum is required to have a shape anticipating the wave-front.

In the case of Fisher Equation, it is the traveling front corresponding to $c = 2$ that plays the role of a global attractor for initial data in the form of the Heaviside function

$$u_0(x) = 1 \quad \text{for } x < 0, \quad u_0(x) = 0 \quad \text{for } x > 0. \quad (5.67)$$

In this case we have (see [3]):

consider Fisher equation (5.32) endowed with the initial datum (5.67). Then there exist a wave-front $\phi(\cdot)$ and a function $\psi(t)$ such that

- $\phi(-\infty) = 1, \quad \phi(+\infty) = 0$;
- $\lim_{t \rightarrow \infty} \psi'(t) = 0$;
- $\lim_{t \rightarrow \infty} |u(t, x) - \phi(x - 2t - \psi(t))| = 0$.

Indeed the asymptotic behavior of solutions depends strongly on the initial datum, and we can also have that the solution approaches wave-fronts proceeding at a speed $c > 2$.

Problems

5.1. The Skellam model for the one-dimensional habitat

The solution of heat equation

$$u_t(t, x) = u_{xx}(t, x) \quad u(0, x) = u_0(x), \quad t \geq 0, \quad x \in (-\infty, +\infty)$$

has the form (see [6], sections 70–71)

$$u(t, x) = \frac{1}{2\sqrt{\pi t}} \int_{-\infty}^{+\infty} e^{-\frac{(x-\xi)^2}{4t}} u_0(\xi) d\xi.$$

Consider the Skellam model (5.7) in a one dimensional habitat.

1. Show that (5.10) is the solution of (5.7) with $u_0(x) = \delta(x)$.
[Hint: show that, if $u(t, x)$ solves (5.7), then $v(t, x) = e^{-t}u(t, x)$ solves the equation above, and then insert the above formula.]
2. In the case of the infinite habitat, discuss the behavior of the range when the growth rate r is negative.
3. Using the separation of variables method (see [6], chapter IV), study population survival in a limited habitat with the following conditions at the border

$$u(t, 0) - h u(t, 0) = 0, \quad u(t, \Lambda) = 0.$$

5.2. The two dimensional habitat

The Skellam equation in a two-dimensional habitat reads

$$u_t = D(u_{xx} + u_{yy}) + ru \tag{5.68}$$

where D is still the diffusion constant and r the growth rate.

1. Consider the diffusion of a population, initially concentrated at the origin, and find the expression for the *range* as a function of time (see Sect. 5.1). For this you should use the fundamental solution of the two dimensional heat equation [6, Sect. 71] and note that the solution has radial symmetry.
2. Consider a rectangular region $\mathcal{R} \equiv [0, L] \times [0, M]$, and suppose the border extremely inhospitable. Find the minimal dimension for the population to survive. Give a sufficient condition for the area of the region to fulfill the previous condition. Suppose that only one of the sides of \mathcal{R} is inhospitable while the other sides of the border are closed, how does the condition for survival change?
3. Consider a circular region of radius R and centered at the origin with extremely inhospitable border. compute the minimum radius for the population to survive.

5.3. The heterogeneous habitat

Consider a one dimensional habitat $[0, L]$ such that there is an internal favorable zone of size Δ surrounded by two unfavorable ones. Suppose then that one species, diffusing in the whole habitat with diffusion constant D , has a growth rate

$$r(x) = \begin{cases} -\mu & \text{for } x \in [0, L_1] , \\ r & \text{for } x \in (L_1, L_1 + \Delta) , \\ -\mu & \text{for } x \in [L_1 + \Delta, L] , \end{cases}$$

where $r > 0$, $\mu > 0$ and $0 < L_1 < L - \Delta$.

1. Suppose extremely inhospitable conditions at $x = 0$ and $x = L$ (Dirichlet conditions) and find the best location (namely x_0) of the favorable region for the species to survive (see the case treated in Sect. 5.4).
2. Do the same as in the previous point with no-flux conditions (Neumann condition) at the border.
3. Consider the limit case $\Delta = L - L_1$, discuss survival as $D \rightarrow 0$ and as $D \rightarrow +\infty$.

5.4. Non-homogeneous equilibria

In Sect. 5.5 we have built a non homogeneous steady state for Fisher equation, satisfying Dirichlet conditions; namely a solution to (5.33) satisfying (5.40). Consider now the same equation (5.33) with the condition

$$U'(0) - h U(0) = 0, \quad U(\Lambda) = 0.$$

1. Draw a phase plane plot showing the graphical meaning of finding such a solution.
2. Sketch the graph of a solution in a picture similar to (5.6). This time you have to split the solution into two non-symmetrical branches, defined on possibly different intervals.
3. Find an equation similar to (5.43), to obtain the left branch implicitly defined and depending on $U(0)$ and u_m . Similarly, find the equation for the right branch.
4. Get the size of the interval as the sum of the two intervals, relative to the two branches.
5. From eq. (5.38) get $U(0)$ as a function of u_m and plug into the previous equation to obtain $\Lambda(u_m)$.

5.5. Traveling fronts for the Allee-logistic model

Consider the Allee-logistic model defined by (5.62) and the corresponding system for the search of wavefronts (system (5.57) with the function $F(\cdot)$ given by (5.63)).

1. Discuss existence of wavefronts looking at trajectories in the phase plane (U, V) , connecting the equilibria $(0, 0)$ and $(\frac{1}{\alpha}, 0)$ or $(\frac{1}{\alpha}, 0)$ and $(1, 0)$.
 2. Find explicit forms of the profiles by the method used in Sect. 5.5.
 3. Discuss and compare the solutions $u(t, x) = \phi(x - ct)$ that you found in the previous question.
-

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Part II

Multispecies Models

Predator-prey models

*Ad rivum eundem lupo et agnus venerant,
siti compulsi. Superior stabat lupo,
longeque inferior agnus. Tunc fauce improba
latro incitatus iurgii causam intulit:
“Cur – inquit – turbulentam fecisti mihi
aquam bibenti?” Laniger contra timens:
“Qui possum – quaeso – facere quod quereris, lupe?
A te decurrit ad meos haustus liquor.”
Repulsus ille veritatis viribus:
“Ante hos sex menses male – ait – dixisti mihi”.
Respondit agnus: “Equidem natus non eram!”
“Pater, hercle, tuus – ille inquit – male dixit mihi”;
Atque ita correptum lacerat iniusta nece.
Haec propter illos scripta est homines fabula
qui fictis causis innocentes opprimunt.¹
Phaedrus, “Lupo et agnus”*

Stories of lambs and wolves have been told since a very long time and the interaction between predators and preys represent the most dramatic aspect of the *struggle for life*². The incipit of Fedro’s fable seems to deal with a case of competition ... for the resource of a *rivum eundem* ... but we should not trust on the wolf’s complaint ... since the beginning of the world wolves are wolves and lambs are lambs ... each of the two species plays a precise role in the scheme of Nature ... the struggle is unfair and the conclusion well expected ...

Predator-prey interaction is a basic mechanism for two species dynamics and mathematical models should explain the many phenomena that in nature are due to

¹ The Wolf and the Lamb/ By thirst incited; to the brook/ The Wolf and Lamb themselves betook./ The Wolf high up the current drank./ The Lamb far lower down the bank./ Then, bent his ravenous maw to cram,/ The Wolf took umbrage at the Lamb./ “How dare you trouble all the flood,/ And mingle my good drink with mud?”/ “Sir,” says the Lambkin, sore afraid,/ “How should I act, as you upbraid?/ The thing you mention cannot be,/ The stream descends from you to me.”/ Abash’d by facts, says he, “I know/ ’Tis now exact six months ago/ You strove my honest fame to blot” –/ “Six months ago, sir, I was not.”/ “Then ’twas th’ old ram thy sire,” he cried,/ And so he tore him, till he died./ To those this fable I address/ Who are determined to oppress,/ And trump up any false pretence,/ But they will injure innocence./ (Translation by Christopher Smart 1913)

² The *struggle for life* came to the fore with Charles Darwin and “*The Origin of Species*”. Later, at the beginning of the twentieth century, *Life Struggle, Struggle for Existence, Lutte pour la Vie* ... were the ways Alfred Lotka, Georgii Frantsevich Gause, Vito Volterra named the subject of their studies (see [6], [8], [16]).

this mechanism. One of the main result is the explanation of abundance oscillation and the unexpected effect of harvesting on complex ecosystems.

This chapter starts with the classical model that Vito Volterra formulated to give an interpretation of the fishery data in the Mediterranean Sea, after the problems posed by the biologist D'Ancona. The same system was also independently analyzed by Alfred Lotka so that it is commonly known as Lotka-Volterra model. It is a rather simple and unrealistic model, but it is able to cast some light on the essentials of the interaction. The subsequent sections of the chapter are then devoted to more refined models and to their consequences. A last section introduces the growth in a chemostat whose dynamics is analogous to the predator-prey case, though the predator consumes non-living resources.

6.1 Volterra model

We consider two species in the same habitat. The first (the *prey*) is the main resource for the other (the *predator*). We suppose that, in the absence of the predator, the prey would undergo a Malthusian growth with a positive rate $r > 0$, while the predator, in the absence of the prey would go extinct with a negative rate $-\mu < 0$. The situation is very different from that of Sect. 1.8, where the prey was experiencing intraspecific competition and the predator was generalist. Here survival of the predator depends on the abundance of the prey (in fact we speak of a *specialist predator*) and the prey has the predator as the unique factor of control. These are extreme assumptions but emphasize typical effects of this kind of species interaction.

Concerning the mechanism of predation, we now need to model both the killing of the preys and the effect on predators growth. Adopting Volterra's formulation of the model we assume a linear response based on the *mass action law* introduced in Sect. 1.8. Namely, we assume that:

- in the time unit, the number of preys consumed by predators is

$$-aH(t)P(t); \quad (6.1)$$

- the total input of new predators in the time unit is

$$\gamma aH(t)P(t) \quad (6.2)$$

where we have denoted by $H(t)$ and $P(t)$ the number of preys and the number of predators, respectively, at time t . Note that (6.1) has the same meaning of (1.30) (in particular a is the attack rate), though in this case the number of predators is not fixed because we are dealing with a specialist predator and we expect its abundance to vary according to prey abundance. The term (6.2), called *numerical response* to predation, is proportional to the number of preys consumed in the unit time and the dimensionless parameter γ , called *conversion rate*, is the pro-capita number of new predators, born in the time unit, for each prey consumed in the same time unit.

With these premises the model is represented by the following system

$$\begin{cases} H'(t) = rH(t) - aH(t)P(t), \\ P'(t) = -\mu P(t) + \gamma aH(t)P(t). \end{cases} \quad (6.3)$$

It is worthwhile interpreting the system in terms of birth and death rates. In fact, the prey and predator growth rates are

$$F(H, P) = r - aP, \quad G(H, P) = \gamma aH - \mu$$

and, splitting the prey intrinsic growth rate as $r = \beta_0 - \mu_0$, we may identify the respective fertility and mortality rate as

$$\beta^H(H, P) = \beta_0, \quad \mu^H(H, P) = \mu_0 + aP,$$

and

$$\beta^P(H, P) = \gamma aH, \quad \mu^P(H, P) = \mu.$$

Moreover, from these we can obtain the respective basic reproduction numbers

$$R_0^H(H, P) = \frac{\beta_0}{\mu_0 + aP}, \quad R_0^P(H, P) = \frac{\gamma aH}{\mu},$$

that now depend on the size of the other population.

System (6.3) has a local solution by the Cauchy existence theorem. From the equations we get

$$H(t) = H(0)e^{\int_0^t (r - aP(s))ds}, \quad P(t) = P(0)e^{\int_0^t (-\mu + \gamma aH(s))ds},$$

so that, since we take $H(0) \geq 0, P(0) \geq 0$, we have $H(t) \geq 0, P(t) \geq 0$. Moreover, we will see that the solution is a priori bounded so that this solution is actually global. This certifies well-posedness of the model.

To have an insight of the solution (and also to prove that it is bounded) we manipulate the equations in (6.3). In fact, if we multiply the first equation by $\mu/H(t)$ and the second by $r/P(t)$, we get

$$\frac{\mu}{H(t)}H'(t) + \frac{r}{P(t)}P'(t) = -a\mu P(t) + r\gamma aH(t),$$

or

$$\frac{d}{dt} (\mu \ln H(t) + r \ln P(t)) = -a\mu P(t) + r\gamma aH(t); \quad (6.4)$$

besides, multiplying the first equation by γa and the second by a , we get

$$\gamma aH'(t) + aP'(t) = -a\mu P(t) + r\gamma aH(t). \quad (6.5)$$

Subtracting (6.4) from (6.5) we obtain

$$\frac{d}{dt}(\gamma a H(t) - \mu \ln H(t) + a P(t) - r \ln P(t)) = 0,$$

so that the quantity in brackets is constant along trajectories, and taking exponentials we end to

$$H^\mu(t) e^{-\gamma a H(t)} P^r(t) e^{-a P(t)} = C,$$

where C is a constant depending on H_0 and P_0 .

Thus, the trajectory of the solutions lies on the curve defined by the equation

$$H^\mu e^{-\gamma a H} P^r e^{-a P} = C. \quad (6.6)$$

Since

$$\lim_{H+P \rightarrow +\infty} H^\mu e^{-\gamma a H} P^r e^{-a P} = 0,$$

we have that the curve is contained in a suitable rectangle (depending on C , i.e. on H_0 and P_0) and is consequently bounded.

We may draw the curve defined by eq. (6.6), using a graphical procedure proposed by Vito Volterra in [16]. To this purpose we consider a change of variables defined by

$$X = H^{-\mu} e^{\gamma a H}; \quad Y = P^r e^{-a P} \quad (6.7)$$

so that, the curve (6.6) is transformed into a line in the new variables X and Y ,

$$Y = CX$$

which is drawn in the octant (X, Y) of Fig. 6.1. In the same figure, in the respective quadrants (H, X) and (P, Y) , we draw the two curves defined in (6.7). With the dashed lines we indicate the procedure that allows to build a cycle in the octant (H, P) (see Fig. 6.1). We note that for either too large or too small values of \bar{H} we fail to intercept the curve in the quadrant (P, Y) so that such values do not correspond to any point on the trajectory.

In Fig. 6.2 we see that the points H_m and H_M correspond to the maximum of the curve Y occurring at $P^* = \frac{r}{a}$, and that the points P_m and P_M correspond to the minimum of the curve X , occurring at $H^* = \frac{\mu}{\gamma a}$. We also understand how the cycles in the octant (H, P) vary with the constant C , which in turn varies with the initial datum (H_0, P_0) . We see that the cycles are encapsulated all around the point

$$E^* = \left(\frac{\mu}{\gamma a}, \frac{r}{a} \right)$$

which is the only non-trivial equilibrium of system (6.3). In fact, the trajectory represented by the single point E^* , is determined by the particular value of C corresponding to the line r_0 (see Fig. 6.1). We note that, since E^* is the only point at which both $H'(t)$ and $P'(t)$ may vanish, any solution runs through a cycle without changing its direction. Finally, to show that each cycle is run periodically, we con-

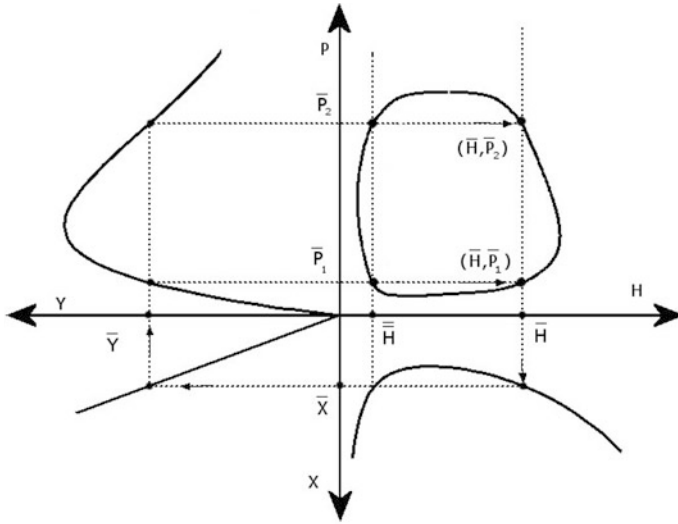


Fig. 6.1 The graphical method by Volterra to draw the trajectories of model (6.3). For a fixed \bar{H} , chosen on the abscissa's axis of the quadrant (H, P) , in order to identify the two points (\bar{H}, \bar{P}_1) and (\bar{H}, \bar{P}_2) lying on the curve, we follow the arrow along the dashed line. Namely, we start in the quadrant (H, X) to compute $\bar{X} = \bar{H}^{-\mu} e^{\gamma a \bar{H}}$, then in the quadrant (X, Y) , we compute $\bar{Y} = C\bar{X}$ and, finally, in the quadrant (P, Y) we identify P_1 and P_2 as the abscissas corresponding to \bar{Y} on the graph of the curve $Y = P^r e^{-aP}$. In conclusion we obtain the sought points. Note that the same values P_1 and P_2 correspond to the abscissa \bar{H}

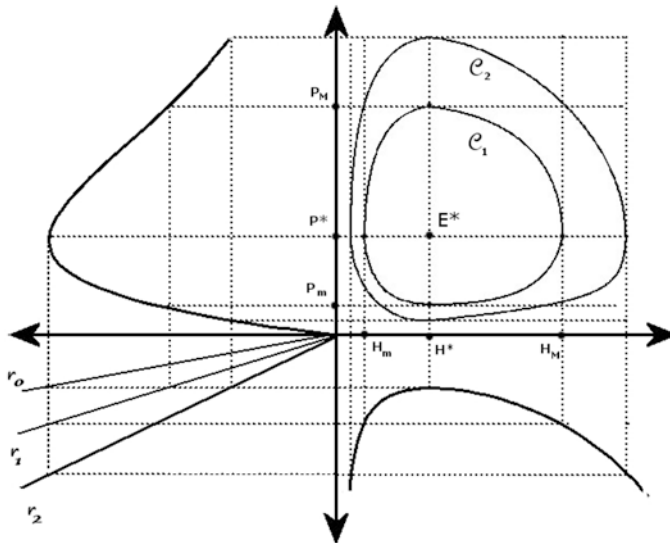


Fig. 6.2 The graphical construction of the trajectories for different values of the initial datum (H_0, P_0) . The different lines r_0, r_1, r_2 correspond to different values of the constant C , i.e. different initial data. For the curve \mathcal{C}_1 , corresponding to r_1 , are shown the minima H_m, P_m and the maxima H_M, P_M . The equilibrium E^* corresponds to the line r_0

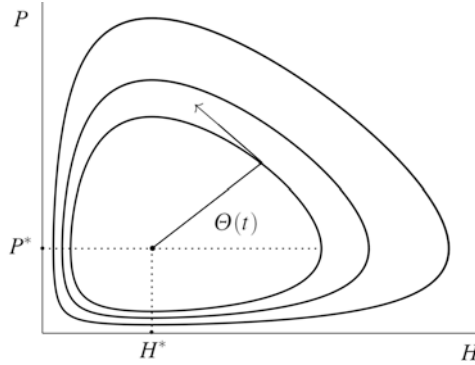


Fig. 6.3 Typical trajectories of the Volterra predator-prey model

sider the vector $(H(t) - H^*, P(t) - P^*)$ and the angle it forms with the H-axis (see Fig. 6.3)

$$\Theta(t) = \arctan \left(\frac{P(t) - P^*}{H(t) - H^*} \right).$$

For this we have

$$\Theta'(t) \geq \min\{\gamma a P_m, a H_m\} > 0, \quad (6.8)$$

so that the vector $(H(t) - H^*, P(t) - P^*)$ makes a complete turn in a finite time, showing that the solution is periodic. Actually it is a general issue that a trajectory, on a closed curve with no equilibria on it, must be the trajectory of a periodic solution (see Problem 6.1). Typical trajectories of the model are shown in Fig. 6.3.

Volterra's model, though rather simple, provides a basic framework to explain the periodic variations, observed in nature, for some species. In Fig. 6.4, we show the data on lynx furs brought to Hudson Bay Company, presumably reflecting the species abundance through the years. These are classical data usually presented as an example of predator-prey interaction, but whose best interpretation is still being examined in recent research papers (see [15] for extended discussions and references on this subject).

Let now T be the period of a solution of system (6.3) and let us compute the average of $H(t)$ and $P(t)$ over one period

$$\bar{H} = \frac{1}{T} \int_0^T H(s) ds \quad ; \quad \bar{P} = \frac{1}{T} \int_0^T P(s) ds. \quad (6.9)$$

Now, from the equation of system (6.3) we have

$$\begin{aligned} 0 &= \ln \frac{H(T)}{H(0)} = \int_0^T (r - aP(s)) ds = rT - a\bar{P}T \\ 0 &= \ln \frac{P(T)}{P(0)} = \int_0^T (-\mu - \gamma aH(s)) ds = -\mu T + \gamma a\bar{H}T \end{aligned}$$

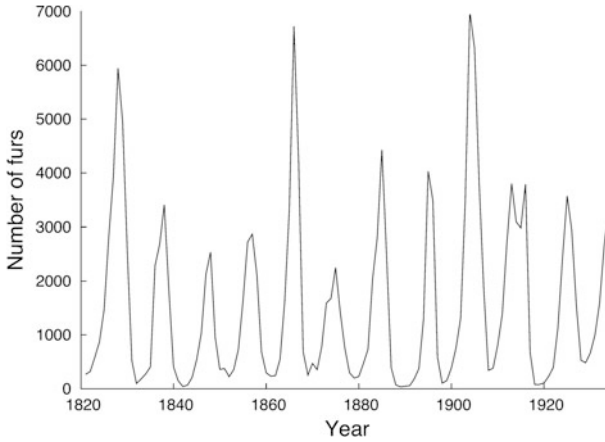


Fig. 6.4 Periodical time variation of lynx fur returns from MacKenzie River region, Northern Canada, during the years 1821–1914. Adapted from [5]

so that

$$\bar{H} = \frac{\mu}{\gamma a} \quad ; \quad \bar{P} = \frac{r}{a}. \quad (6.10)$$

We then see that the averages (6.9) coincide with the coordinates of E^* and do not depend on the initial datum (H_0, P_0) . We see that in this model the ecosystem stays on a sort of natural equilibrium though the abundance of each species is not constant and the amplitude of oscillations depends on the initial datum. The average values depends only on the parameters describing species interaction.

Formulae (6.10) are also a key-tool to analyze the effect of harvesting on the ecosystem by examining how they vary under a constant killing effort exerted on the whole system. Here killing may mean fishing, hunting, pollution, or the spreading of pesticides and, in order to model this external action we introduce:

- αE = specific killing rate of the prey;
- βE = specific killing rate of the predator.

Here the parameter E represents the effort (see Sect. 1.10), while α and β are a measure of the returns (in general different) relative to each species. System (6.3) is modified into

$$\begin{cases} H'(t) = [r - \alpha E - aP(t)]H(t), \\ P'(t) = [-\mu - \beta E + \gamma aH(t)]P(t). \end{cases}$$

Provided that $r > \alpha E$, these additional terms do not modify the structure of the dynamics but introduce changes in the parameters of the system. The coordinates of

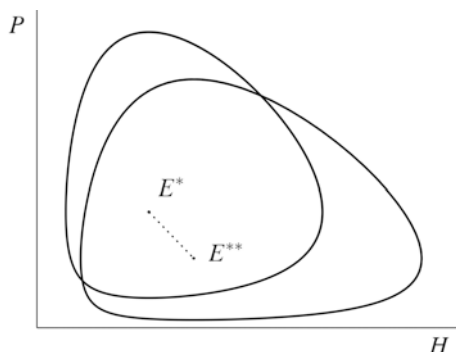


Fig. 6.5 Volterra's principle: the equilibrium E^* shifts right down to E^{**}

E^* modify into

$$H^{**} = \frac{\mu + \beta E}{\gamma a} \quad ; \quad P^{**} = \frac{R - \alpha E}{a},$$

and we see that an increase of the effort E produces a decrease of the predator and an increase of the prey (see Fig. 6.5).

The conclusion drawn from the previous analysis were summarized by Volterra himself in three basic laws:

- **Law of periodic cycle:**
the fluctuations of the two species are periodic;
- **Law of conservation of averages:**
the averages of the numbers of the individuals of the two species over a period of time are constant and do not depend upon initial values;
- **Law of perturbation of averages:**
if the two species are uniformly destroyed proportionally to the number of their individuals, the average of the number of individuals of the devoured species increases and the average of the number of individuals of the devouring species decreases.

The third law, also called Volterra's principle, is important to understand the effect of human intervention on the ecosystems. Actually, the interest of Volterra for this problem arose from features of fishery data collected by Umberto D'Ancona. In fact data showed evidence that, during the World War I, in the Adriatic sea, the frequency of predators had an anomalous increase (see Fig. 6.6). The explanation provided by Volterra is that the decrease of fisheries during the war had modified the equilibrium in favor of predators moving back from E^{**} to E^* .

Another important application related to Volterra's principle is the use of insecticides on insect populations that are controlled by insect predators. In fact the pes-

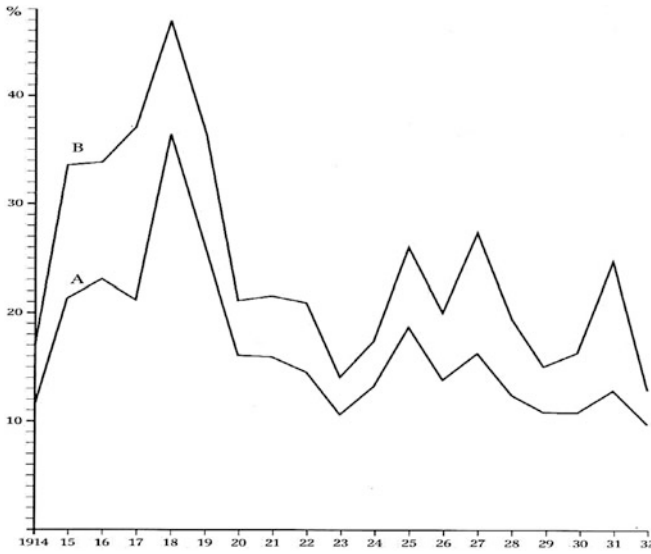


Fig. 6.6 D'Ancona's data on Mediterranean fisheries, concerning selachians (predators). Curve A reports the ratio of selachians on the total of benthic fishes, cephalopods and crustacean; curve B the ratio on the total of benthic fishes only. A peak occurs during the years of World War I. From [4]

ticide may shift the equilibrium point so to cause the prey (at which the insecticide is aimed) to have an unexpected increase.

In spite of the success of the Volterra model in explaining the mechanism of predator-prey interaction, we must say that the extreme simplifications make the model weak. In particular, as we have already discussed, the constitutive form of the functional response to predation, based on the encounter mechanisms and inspired to the law of mass action has been strongly criticized. The more complex models arising from other functional responses of the types already presented will be the subject of the subsequent sections.

6.2 Prey with Verhulst-logistic growth

Here we consider a variation of Volterra model that keeps the mass-action law for the predator, but assumes that in the absence of predators the prey undergoes logistic growth with a Verhulst type growth rate instead of a Malthusian one. Namely we consider the model

$$\begin{cases} H'(t) = r \left(1 - \frac{H(t)}{K} \right) H(t) - aH(t)P(t), \\ P'(t) = -\mu P(t) + \gamma aH(t)P(t) \end{cases} \quad (6.11)$$

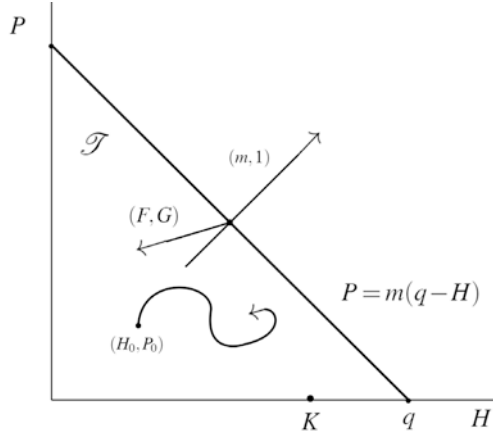


Fig. 6.7 Boundedness of solutions to the Volterra-Verhulst model

where the prey and the predator have the respective growth rates

$$F(H, P) = r \left(1 - \frac{H(t)}{K} \right) - aP; \quad G(H, P) = -\mu + \gamma aH.$$

A few first remarks concern well-posedness of this model. In fact, as in the case of system (6.3) we can easily prove that $H(t) \geq 0$, $P(t) \geq 0$ if $H(0) \geq 0$ and $P(0) \geq 0$. Moreover, we can prove boundedness of any solution showing that any trajectory is contained in the triangle \mathcal{T} formed by the lines

$$H = 0, \quad P = 0, \quad P = m(q - H)$$

for suitable m and q (see Fig. 6.7). To this purpose, we may first note that the lines $H = 0$ and $P = 0$ are invariant, so that any trajectory starting from a point (H_0, P_0) in the interior of \mathcal{T} cannot cross the boundary at these lines. Furthermore, noticing that an outer normal of the line $P = m(q - H)$ has components $(m, 1)$, we compute its scalar product with the differential field of (6.11) at any point (H, P) on this line. We have

$$\begin{aligned} (F(H, P)H, G(H, P)P) \cdot (m, 1) &= \\ &= mrH - m \frac{r}{K} H^2 - maHP - \mu P + \gamma aHP = \\ &= mr \left(1 - \frac{q}{K} \right) H + m \frac{r}{K} (q - H)H - \mu P - (am - a\gamma)HP, \end{aligned}$$

where we have added and subtracted $mrqH/K$. Then, substituting $P = m(q - H)$, we get

$$\begin{aligned} (F(H, P)H, G(H, P)P) \cdot (m, 1) &= \\ &= mr \left(1 - \frac{q}{K} \right) H - \mu P - \left(-\frac{r}{K} + am - a\gamma \right) HP < 0 \end{aligned}$$

provided we take $q > K$ and $m > \gamma + \frac{r}{aK}$. Thus the differential field points to the interior of \mathcal{T} and the trajectory cannot cross the boundary at any point of the line. Having proved that the solution is bounded we can conclude that it is global and that the model is well-posed.

Next we look for steady states. It is easy to see that the *extinction state* $E_0 \equiv (0, 0)$ is unstable (see Appendix A). In fact the Jacobian matrix at this point

$$J(E_0) = \begin{pmatrix} r & 0 \\ 0 & -\mu \end{pmatrix}$$

shows that it is a saddle point, with the axes $H = 0$ and $P = 0$ as stable and unstable manifold respectively.

Furthermore we have the *exclusion state* $E_K \equiv (K, 0)$, corresponding to predator extinction, and a *coexistence equilibrium* $E^* \equiv (H^*, P^*)$ with components

$$H^* = \frac{\mu}{\gamma a}, \quad P^* = \frac{r}{a} \left(1 - \frac{\mu}{\gamma a K} \right) = \frac{r}{a} \left(1 - \frac{H^*}{K} \right), \quad (6.12)$$

that exists only if

$$H^* = \frac{\mu}{\gamma a} < K. \quad (6.13)$$

Concerning the stability of E_K , the Jacobian is

$$J(E_K) = \begin{pmatrix} -r & -aK \\ 0 & \gamma a(K - H^*) \end{pmatrix}.$$

The eigenvalues of $J(E_K)$ are the two element of the diagonal, so E_K is stable for $H^* > K$, unstable for $H^* < K$, i.e. it is unstable when E^* exists (by condition (6.13)). On the other hand

$$J(E^*) = \begin{pmatrix} -\frac{r}{K}H^* & -aH^* \\ \gamma aP^* & 0 \end{pmatrix},$$

and $\det J(E^*) > 0$, $\text{Trace} J(E^*) < 0$, so E^* is asymptotically stable whenever it exists. In Fig. 6.8 the equilibria in the two cases are shown together with the position of the isoclines of the system. The previous discussion is summarized as:

for system (6.11) the extinction equilibrium $E_0 = (0, 0)$ is unstable and the exclusion equilibrium $E_K = (K, 0)$ is stable for $H^* > K$, unstable for $H^* < K$. When E_K is unstable a stable coexistence equilibrium $E^* = (H^*, P^*)$ exists.

Concerning the behavior of solutions, we have more than simple asymptotic stability of equilibria, because in both cases the behavior is global. Consider first the case $H^* > K$ illustrated in Fig. 6.9-(a), where the vector field of system (6.11) is also represented and the key regions (\mathcal{A} , \mathcal{B} , \mathcal{C}) of the phase space are identified. Since we have proved that the solution is bounded in the triangle \mathcal{T} , and since we

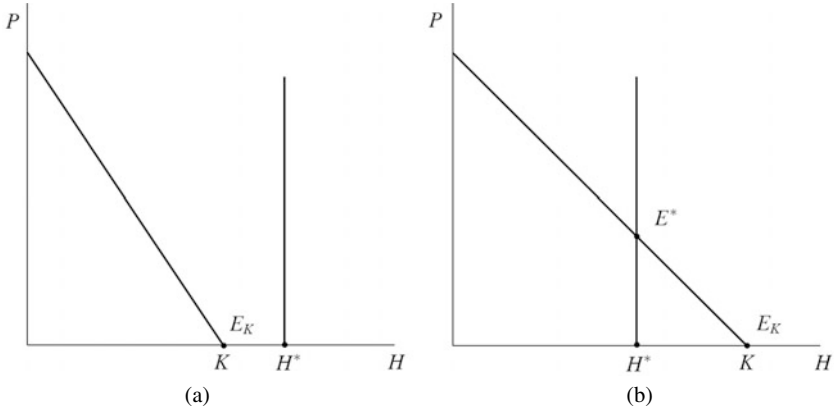


Fig. 6.8 Non-trivial steady states for the Volterra-logistic model: (a) the case $H^* > K$ when only the exclusion state $E_K \equiv (K, 0)$ exists and is stable (a stable node); (b) the case $H^* < K$ when E_K is a saddle point, E^* exists, bifurcating from E_K at $H^* = K$, and is stable

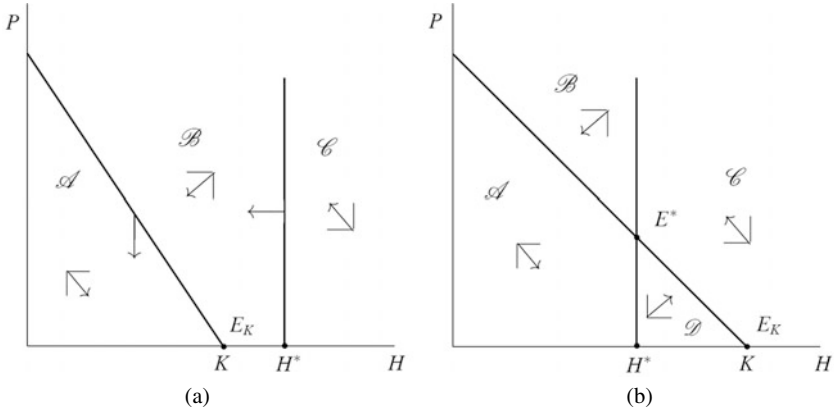


Fig. 6.9 The differential field of the Volterra-Verhulst model: (a) $H^* > K$; (b) $H^* < K$

can exclude the existence of periodic orbits because there are no equilibria in the interior of \mathcal{T} , by the Poincaré-Bendixson theorem, the ω -limit set of any trajectory must contain an equilibrium point (see Appendix A). Now, from the orientation of the vector field we have (see Fig. 6.9-(a)):

- if $(H_0, P_0) \in \mathcal{A}$, then the trajectory stays in $\mathcal{A} \cap \{H \geq H_0\}$ and tends to E_K which is the only available equilibrium point;
- if $(H_0, P_0) \in \mathcal{B}$, then the trajectory either stays in \mathcal{B} and tends to E_K which is again the only available equilibrium point, or passes into \mathcal{A} and tends to E_K , as shown before;
- if $(H_0, P_0) \in \mathcal{C}$, then the trajectory must pass into \mathcal{B} in a finite time, because in \mathcal{C} there is no equilibrium point. Thus it tends to E_K , as shown before.

In conclusion we have:

if $K \leq H^* = \frac{\mu}{\gamma a}$, then $E_K \equiv (K, 0)$ is the only non-trivial equilibrium and, for any initial datum (H_0, P_0) with $H_0 > 0$ and $P_0 > 0$, we have

$$\lim_{t \rightarrow \infty} (H(t), P(t)) = (K, 0) .$$

Note that if $P_0 = 0$ there is no predator and the prey grows with no interference, attaining its carrying capacity. Note also that H^* is a threshold value for the prey abundance to sustain the predator growth. In fact

$$G(H, P) = -\mu + \gamma a H$$

is negative or positive according to whether $H < H^*$ or $H > H^*$. If we consider the basic reproduction number of the predator at the equilibrium E_K , we have

$$R_0^P(E_K) = \frac{\gamma a K}{\mu} = \frac{K}{H^*},$$

showing that the condition $K > H^*$ means $R_0^P(E_K) > 1$ and is a condition for the predator to invade the habitat where the prey has attained its carrying capacity.

We now consider the case $H^* < K$ illustrated in Fig. 6.9-(b). In this case we identify the four regions \mathcal{A} , \mathcal{B} , \mathcal{C} and \mathcal{D} relative to different orientations of the differential field, possibly allowing trajectories to cross infinite times from one region to another. However we can exclude existence of periodic orbits by the Bendixson-Dulac criterion (see Appendix A). In fact, taking $D(H, P) = (HP)^{-1}$ as a Dulac function, we have

$$\operatorname{div} \left(\frac{1}{P} F(H, P), \frac{1}{H} G(H, P) \right) = -\frac{r}{PK} < 0.$$

Thus, no periodic or heteroclinic orbit exists and, since the only trajectories converging to the saddle points E_0 or E_K are the axes $H = 0$ and $P = 0$, by the Poincaré-Bendixson Theorem, the ω -limit set of any other trajectory must be an equilibrium point, i.e. E^* . Thus we conclude:

if $K > H^* = \frac{\mu}{\gamma a}$, then for any initial datum (H_0, P_0) , with $H_0 > 0$ $P_0 > 0$, we have

$$\lim_{t \rightarrow \infty} (H(t), P(t)) = E^* \equiv (H^*, P^*).$$

We note that the same results could be obtained using the Lyapunov function

$$V(H, P) = \gamma(H - H^* \log H) + P - P^* \log P.$$

In fact this function is *not-increasing along the solutions* since

$$\dot{V}(H, P) = -\frac{r\gamma}{K}(H - H^*)^2 \leq 0.$$

Application of the La Salle theorem (see Appendix A) makes one reach the conclusion. In fact this theorem guarantees that the ω -limit set of a trajectory lies on the line

$$H = H^*$$

and, since the only invariant set contained in this line is the equilibrium $E^* = (H^*, P^*)$, then E^* is the ω -limit set of any trajectory.

This method to prove global asymptotic stability is more complex than the use of the Dulac function. However, the function $V(H, P)$, or slightly modified versions, are Lyapunov functions in several ecological or epidemiological systems, also of higher dimensions, where they constitute an essential tool.

The previous model shows that if the prey does not undergo Malthusian growth, but has a carrying capacity, no matter how large, the periodic solutions provided by the Volterra model disappears. Mathematically, this means that Lotka-Volterra model (6.3) is not structurally stable, since arbitrary small modification may substantially change the behavior of solutions.

An important observation is that however Volterra's principle still holds, since introducing a harvesting term in the model is equivalent to decreasing r and increasing μ , thus increasing H^* and decreasing P^* (see (6.12)).

We may also discuss how P^* varies with the attack rate a , that gives a measure of how fast, voracious or capable of catching a prey the predator is. In fact, from (6.12) we have

$$P^*(a) = \frac{r}{a} \left(1 - \frac{\mu}{\gamma K a} \right), \quad \text{for } a \geq \frac{\mu}{\gamma K}.$$

The plot of $P^*(a)$ is shown in Fig. 6.10. Actually P^* has a maximum at $a_{opt} = \frac{2\mu}{\gamma K}$ and this value would correspond to the optimal strategy for the species to have the

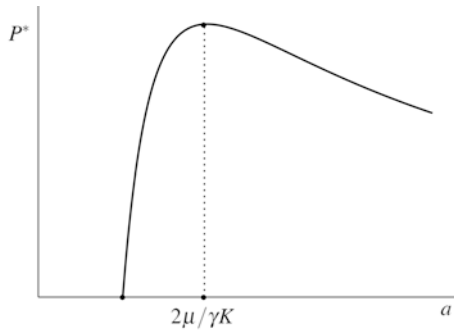


Fig. 6.10 Volterra-Verhulst model: the predator abundance at equilibrium, as a function of the attack rate a

maximum abundance. Of course the optimal strategy (wise predators) is advantageous for the species as a whole and not for the single predator that would probably be selected for an increasingly large attack rate. This type of problems, belonging to evolutionary ecology, are not analyzed in this book.

The model presented in this section is a particular case of a class of predator-prey models that may be considered adequate for describing this interaction. This class, named Gause-type models after G.F. Gause [6] who introduced it also in connection with laboratory experiments, will be considered in the next section.

6.3 Gause-type models

Gause type models have following general form

$$\begin{cases} H'(t) = r(H(t))H(t) - \pi(H(t))P(t) \\ P'(t) = -\mu P(t) + \omega(H(t))P(t) \end{cases} \quad (6.14)$$

and are intended to describe the interaction of a prey with a specialist predator. In fact as we will see, in the absence of the prey ($H(0) = 0$) the predator undergoes extinction. Each item in (6.14) has its ecological meaning and some of them have been already introduced and discussed in the previous sections. The list below summarizes the meaning and properties of each rate:

- **$r(H)$: prey growth rate**
this term describes the growth of the prey in the absence of predators and in general it may include all the possible intraspecific effect discussed in the previous sections, such as a pure logistic behavior and/or an Allee effect. The assumptions on $r(H)$ may then be (1.18) or (1.23). More frequently the prey growth rate is modeled with a simple Verhulst rate such as (1.19);
- **μ : intrinsic mortality rate of the predator**
we assume that without preys, the predator goes to extinction and the average life length is $\tau = 1/\mu$;
- **$\pi(H)$: functional response to predation**
the meaning of this term has been sufficiently discussed in Chap. 1 and used in the analysis of generalist predation. We recall the general properties (1.32) and the specific forms (1.33) largely used in specific modeling;
- **$\omega(H)$: numerical response to predation**
this is the number of new predators produced in the time unit by a single predator. It is usually assumed to be an increasing function of the functional response $\pi(H)$, and, in general, it is assumed

$$\omega'(H) \geq 0, \quad \lim_{H \rightarrow +\infty} \omega(H) > \mu. \quad (6.15)$$

In the analysis we will also use the function

$$\pi_0(H) = \frac{\pi(H)}{H}$$

that gives the *fraction of preys captured in the time unit by one predator* and satisfies $\pi_0(0) = \pi'(0)$.

Condition (6.15) is necessary to avoid the trivial case of a predator with a negative growth rate at any abundance of the prey. Namely, (6.15) guarantees the existence of a unique value $H = T_H$ satisfying

$$\omega(T_H) = \mu. \quad (6.16)$$

Often the numerical response is assumed to be proportional to the functional response

$$\omega(H) = \omega_0 \pi(H),$$

where ω_0 is a positive dimensionless constant that can be interpreted as converting captured preys into new predators. We note that, while the form of the functional response is based on a description of the mechanism of predation and also supported by experimental data, the form of the numerical response $\omega(H)$ has not been discussed thoroughly and is usually simply motivated by the idea that the abundance of captured preys should produce a proportional return in terms of fertility. More realistically, one would expect that the reproduction rate of predators would depend on the average number of preys captured in the near past, and not on instantaneous abundance of preys. Such a model would be mathematically more complex.

From the general assumptions listed above some basic results follow concerning existence and local stability of equilibria for model (6.14). To perform the analysis we assume that the assumption (1.23) is satisfied with $r(0) > 0$ and that (1.32), (6.15) are fulfilled. We first note that we still have the two equilibria

$$E_0 \equiv (0, 0), \quad E_K \equiv (K, 0).$$

Moreover we consider the isoclines given by the curves

$$\begin{aligned} H &= T_H, \\ P &= \phi(H) = \frac{r(H)}{\pi_0(H)}, \quad H \in [0, K], \end{aligned}$$

In Fig. 6.11 these isoclines are shown in the two cases $K < T_H$ and $K > T_H$; thus we see that T_H , defined in (6.16), has the role of a threshold and we conclude that:

if $K < T_H$ there exist only the equilibria E_0 and E_K . If $K > T_H$ an additional coexistence equilibrium $E^* \equiv (H^*, P^*)$ exists, with

$$H^* = T_H, \quad P^* = \phi(T_H) = \frac{r(T_H)}{\pi_0(T_H)}.$$

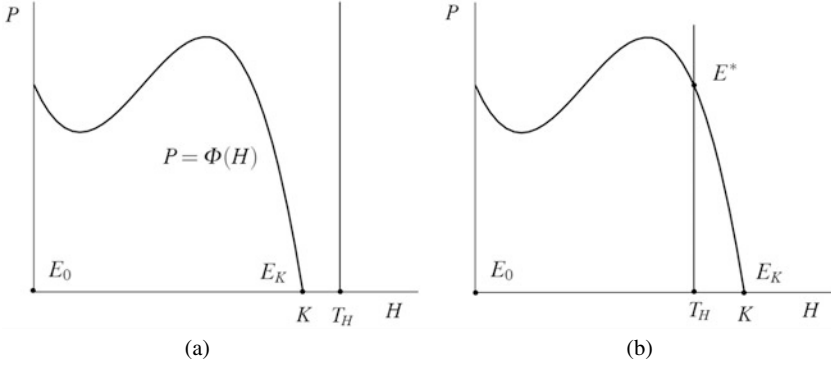


Fig. 6.11 Non-trivial steady states for the Gause model: (a) the case $K < T_H$ when only the extinction states $E_0 \equiv (0,0)$ and $E_K \equiv (K,0)$ exist; (b) here $K > T_H$ and an additional coexistence state E^* exists

Concerning the stability of these equilibria we can easily compute the respective Jacobian matrices

$$J(E_0) = \begin{pmatrix} r(0) & 0 \\ 0 & -\mu \end{pmatrix},$$

$$J(E_K) = \begin{pmatrix} r'(K)K & -\pi(K) \\ 0 & -\mu + \omega(K) \end{pmatrix}$$

and

$$J(E^*) = \begin{pmatrix} \phi'(T_H)\pi(T_H) & -\pi(T_H) \\ \omega'(T_H)\frac{\varepsilon(T_H)}{\pi_0(T_H)} & 0 \end{pmatrix}.$$

Thus we see that E_0 is always unstable while E_K is stable if $K < T_H$, unstable otherwise (in this case it is a saddle point).

Concerning E^* we see that, since the determinant of $J(E^*)$ is positive, it is not a saddle point and it is asymptotically stable if and only if $\phi'(T_H) < 0$, thus (see Fig. 6.12):

the stability of E^* , is determined by the slope of the tangent to the isocline $P = \phi(H)$ at E^* : if the slope is negative, then E^* is asymptotically stable, if it is positive, E^* is unstable.

Under the general assumption we have been considering up to now, it is not possible to draw results on the global behavior of the solutions. However, in specific cases, it is possible to prove boundedness of solutions. In that case, when E^* is unstable, Poincaré-Bendixson theorem allow to conclude that a periodic orbit must exist around E^* . We cannot exclude that more than one periodic orbit surrounds E^* both if it is stable and if it is unstable. More specific forms of the ingredients of the

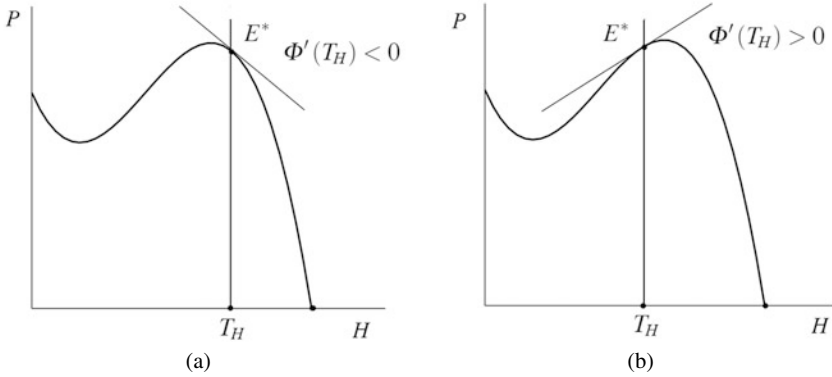


Fig. 6.12 Stability of the coexistence equilibrium E^* : (a) $\phi'(T_H) < 0$ and E^* is asymptotically stable; (b) $\phi'(T_H) > 0$ and E^* is unstable

model allow to get more precise conclusions. This is the case of the model we will consider in the next section.

6.4 The Rosenzweig-MacArthur model

A particular choice of the rates in the Gause-type model allows to have a complete description of the dynamics. The Rosenzweig-MacArthur model (see [12]) is an evolution of the Volterra-Verhulst model in that the linear functional response is replaced by a Holling II response. Thus we have the model³

$$\begin{cases} H'(t) = r \left(1 - \frac{H(t)}{K} \right) H(t) - \frac{aH(t)}{1 + a\tau H(t)} P(t), \\ P'(t) = -\mu P(t) + \gamma \frac{aH(t)}{1 + a\tau H(t)} P(t), \end{cases}$$

which is a particular Gause model with

$$r(H) = r \left(1 - \frac{H}{K} \right), \quad \pi(H) = \frac{aH(t)}{1 + a\tau H(t)}, \quad \omega(H) = \gamma\pi(H),$$

where we assume (see condition (6.15))

$$\lim_{H \rightarrow \infty} \omega(H) = \frac{\gamma}{\tau} > \mu. \quad (6.17)$$

³ Actually in [12] the model is not explicitly formulated in terms of differential equations. Nevertheless the model is usually named after Rosenzweig and MacArthur because the shape of the isocline reflects the graphical description discussed in the paper.

With these assumptions we have

$$T_H = \frac{\mu}{a(\gamma - \mu\tau)}$$

and the isocline $\phi(H)$ is a part of the parabola (see Fig. 6.13)

$$\phi(H) = \frac{r}{aK}(K - H)(1 + a\tau H), \quad H \in [0, K]$$

with its vertex at

$$H_V = \frac{a\tau K - 1}{2a\tau}.$$

Then we have:

let condition (6.17) be satisfied. If $H_V < T_H < K$, a unique coexistence equilibrium E^* exists and, for any initial datum $H_0 > 0, P_0 > 0$,

$$\lim_{t \rightarrow +\infty} (H(t), P(t)) = E^*; \quad (6.18)$$

if $T_H < H_V$, the unique coexistence equilibrium E^* is unstable and a unique globally attractive periodic solution exists.

To prove this statement we first consider the case $H_V < T_H < K$ and note that from the general discussion held in the previous section we obtain existence, uniqueness and stability of a coexistence equilibrium E^* (see Fig. 6.13 where the case $H_V > 0$ is shown, but it could also be $H_V \leq 0$ without any changes). To prove global stability

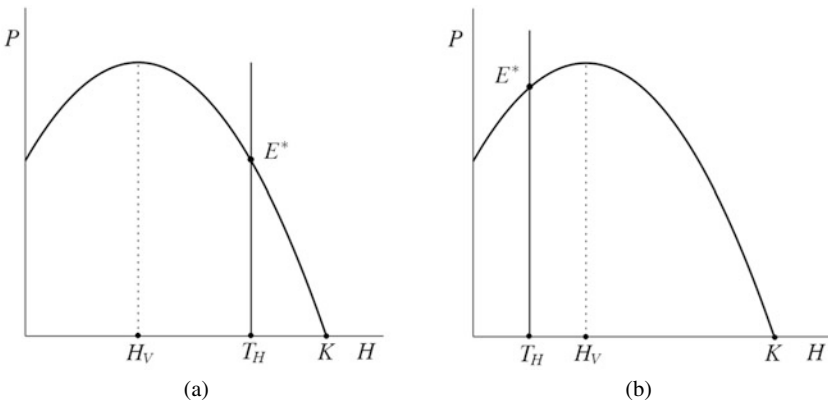


Fig. 6.13 Phase plane for the Rosenzweig-MacArthur model: (a) the case $H_V < T_H < K$; no periodic solutions exist and E^* is globally attractive; (b) the case $T_H < H_V$; E^* is unstable and a unique periodic solution exists

we only need to exclude existence of periodic orbits. Now, by the Dulac function

$$D(H, P) = \frac{1 + a\tau H}{H} P^{\alpha-1} \quad \text{with} \quad \alpha = \frac{2ra\tau T_H}{K\mu} |H_V|,$$

we have

$$\begin{aligned} \mathbf{Div}(D(H, P)HF[H, P], D(H, P)PG[H, P]) &= \\ &= \frac{2a\tau r}{K} P^{\alpha-1} (H_V - H) + \frac{\alpha\mu}{HT_H} P^{\alpha-1} (H - T_H) = \\ &= -\frac{2a\tau r}{HK} P^{\alpha-1} (H^2 - (H_V + |H_V|)H + |H_V|T_H). \end{aligned} \quad (6.19)$$

Thus, if $H_V \leq 0$,

$$\begin{aligned} \mathbf{Div}(D(H, P)HF[H, P], D(H, P)PG[H, P]) &= \\ &= -\frac{2a\tau r}{HK} P^{\alpha-1} (H^2 - T_H H_V) < 0, \end{aligned}$$

while, if $H_V > 0$, for $H \neq H_V$ we have

$$\begin{aligned} \mathbf{Div}(D(H, P)HF[H, P], D(H, P)PG[H, P]) &= \\ &= -\frac{2a\tau r}{HK} P^{\alpha-1} (H^2 - 2HH_V + H_V T_H) \leq \\ &\leq -\frac{2a\tau r}{HK} P^{\alpha-1} (H^2 - 2HH_V + H_V^2) = \\ &= -\frac{2a\tau r}{HK} P^{\alpha-1} (H - H_V)^2 < 0, \end{aligned}$$

where we have used $H_V \leq T_H$.

Concerning the case $H_V > T_H$, instability of E^* and existence of a periodic solution follow from the general results for Gause-type models. Uniqueness of the periodic solution is somewhat complicated and will be omitted; the complete proof of the statement can be found in [3].

The above results concerning Rosenzweig-MacArthur model can be summarized in a bifurcation graph. To this purpose we scale the system through the transformation

$$t \rightarrow \tilde{t} = \mu t, \quad H \rightarrow u = \frac{H}{K}, \quad P \rightarrow v = \frac{P}{\gamma K}$$

to obtain

$$\begin{cases} u'(t) = \rho(1 - u(t))u(t) - \frac{\alpha\delta u(t)}{1 + \delta u(t)}v(t), \\ v'(t) = \left(\frac{\alpha\delta u(t)}{1 + \delta u(t)} - 1 \right)v(t), \end{cases} \quad (6.20)$$

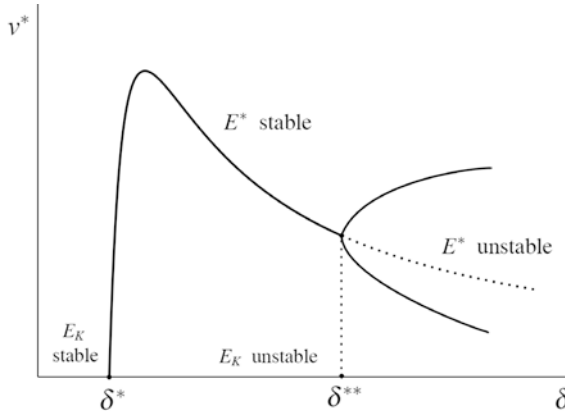


Fig. 6.14 Bifurcation graph for the dimensionless Rosenzweig-MacArthur model (6.20). For $\delta < \delta^*$ there exist only the exclusion equilibrium E_K which is globally asymptotically stable. At δ^* the coexistence equilibrium E^* bifurcates from E_K and inherits its stability. At δ^{**} Hopf bifurcation occurs, E^* becomes unstable and a unique globally attractive periodic solution exists

where

$$\rho = \frac{r}{\mu}, \quad \alpha = \frac{\gamma}{\tau\mu}, \quad \delta = a\tau K,$$

and $\alpha > 1$ in order to fulfill (6.17). Actually, choosing δ as a bifurcation parameter we have the graph of Fig. 6.14, where the switching values are

$$\delta^* = \frac{1}{\alpha - 1}, \quad \delta^{**} = \frac{\alpha + 1}{\alpha - 1}.$$

Since the bifurcation parameter δ is proportional to K , while the other parameters are independent of it, the bifurcation graph describes the so called *paradox of enrichment* as it was formulated by Rosenzweig in [13]. The paradox amounts to say that an improvement of the life conditions of the prey may have the effect of destabilizing the system. In Rosenzweig's own words:

... increasing the supply of limiting nutrients or energy tends to destroy the steady state; thus man must be careful in attempting to enrich an ecosystem in order to increase its food yield. ...

In Gause's models, one may observe another general effect of the enrichment that, in our view, is actually more paradoxical. In fact, when the equilibrium E^* exists, the abundance of the prey, at this equilibrium, does depend only on the parameters of the predator. In particular it is not affected by the carrying capacity K , hence, if we increase the supply of energy to an ecosystem we would not produce any increase of the prey abundance, but only give an advantage for the predator to grow.

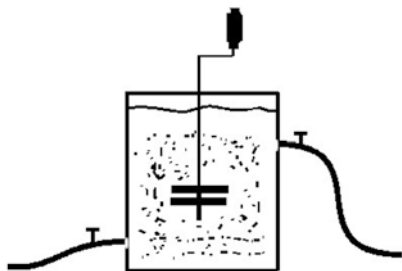


Fig. 6.15 The chemostat: a container with a fluid continuously stirred to guarantee homogeneous mixing, and a continuous input and output of fluid in order to convey nutrient and renew the environment of the culture

6.5 Growing bacteria in a chemostat

The ideas developed in the previous sections have obtained a fruitful applications in describing the growth of micro-organisms (as bacteria or dye) in a *chemostat*.

A chemostat, roughly sketched in Fig. 6.15, is an experimental device designed to grow micro-organisms under controlled conditions. It consists of a container with a fluid continuously stirred to guarantee homogeneous mixing, and a continuous input and output of fluid in order to convey nutrient and renew the environment of the culture (see [10] and [11] for early presentations).

Chemostats are used for the production of large volumes of cells or cell's products, for industrial aims, but also to study the dynamics of interacting species. The simplest case we may consider is the growth of a single species (such as bacteria or other micro-organisms) under a constant influx of nutrient, while life conditions are kept constant. The resulting model actually belongs to the class of predator-prey models since the nutrient can be considered a prey and the species feeding on it a predator.

Let $N(t)$ be the number of individuals in the chemostat and $C(t)$ be the nutrient concentration inside the container. The assumptions and the parameters determining the dynamics are:

- **V : volume of the container**
the volume of the suspension of the culture (dimensions $[l^3]$);
- **ϕ : flux of the liquid**
the volume of liquid getting in and out of the container in unit time (dimensions $[l^3 \times t^{-1}]$);
- **C_0 : nutrient concentration**
the nutrient enters into the device through the incoming flux at a constant concentration (dimensions $[m \times l^{-3}]$);

- $\pi(m)$: **functional response**

the per capita uptake of nutrient by the population is a function of the mass m of the total nutrient contained in the chemostat (dimensions $[m \times N^{-1} \times t^{-1}]$) through a Holling II type functional response

$$\pi(m) = \frac{am}{1 + a\tau m}, \quad (6.21)$$

where a is the **uptake rate** (dimensions $[N^{-1} \times t^{-1}]$) and τ (dimensions $[t \times N \times m^{-1}]$) the time for consuming the pro-capita mass of nutrient;

- γ : **conversion parameter**

each new individual of the population corresponds to a fixed amount of up-taken nutrient. This parameter converts nutrient mass into newborns (dim. $[N \times m^{-1}]$);

- μ : **intrinsic mortality**

we assume that bacteria die with a constant intrinsic mortality, though it may be very low with respect to the speed of the process (dim. $[t^{-1}]$).

Here $[l]$ and $[m]$ denote dimensions of *length* and *mass* respectively. We note that in this context, the form (6.21) for the pro-capita uptake was introduced in [10] with different motivations and is known as *Monod law*.

Now, the mass balance of the nutrient provides the equation

$$VC'(t) = \phi C_0 - \phi C(t) - \pi(VC(t))N(t).$$

Similarly, since we have to take into account the loss of individuals due to the outgoing flux, at a rate $\phi N(t)/V$, we have

$$N'(t) = (-\mu + \gamma\pi(VC(t)))N(t) - \frac{\phi}{V}N(t).$$

Then, adopting new dimensionless variables by the transformation

$$t \rightarrow \tilde{t} = \frac{\phi}{V} t, \quad C \rightarrow u = \frac{C}{C_0}, \quad N \rightarrow v = \frac{N}{\gamma VC_0},$$

we get the dimensionless system (for not overloading the notations we use again t instead of \tilde{t})

$$\begin{cases} u'(t) = 1 - u(t) - h(u(t))v(t), \\ v'(t) = (h(u(t)) - 1 - \tilde{\mu})v(t) \end{cases} \quad (6.22)$$

where

$$\tilde{\mu} = \frac{V}{\phi}\mu,$$

$$h(x) = \frac{Ax}{1+Bx}, \text{ with } A = \frac{aC_0V^2\gamma}{\phi}, \quad B = a\tau VC_0. \quad (6.23)$$

Note that both A and B are dimensionless and, in order to avoid the trivial case of bacteria going extinct because the growth rate is always negative, we assume

$$\lim_{x \rightarrow +\infty} h(x) = \frac{A}{B} > 1 + \tilde{\mu}. \quad (6.24)$$

Model (6.22) belongs to the class of Gause-type models with

$$r(u) = \frac{1}{u} - 1$$

and can be analyzed with the same arguments. Well-posedness of the model can be proved as in Sect. 6.2 and it is easy to draw the isoclines

$$u = u^* = \frac{1 + \tilde{\mu}}{A - (1 + \tilde{\mu})B}, \quad v = \frac{(1 - u)(1 + Bu)}{Au},$$

with the vector field, to find equilibria and discuss their stability. Figure 6.16 summarizes the situation and we can eventually state the following conclusion:

consider system (6.22) with condition (6.24). If $u^* > 1$, then

$$\lim_{t \rightarrow +\infty} (u(t), v(t)) = (1, 0);$$

if $u^* < 1$, then

$$\lim_{t \rightarrow +\infty} (u(t), v(t)) = E^* = (u^*, v^*).$$

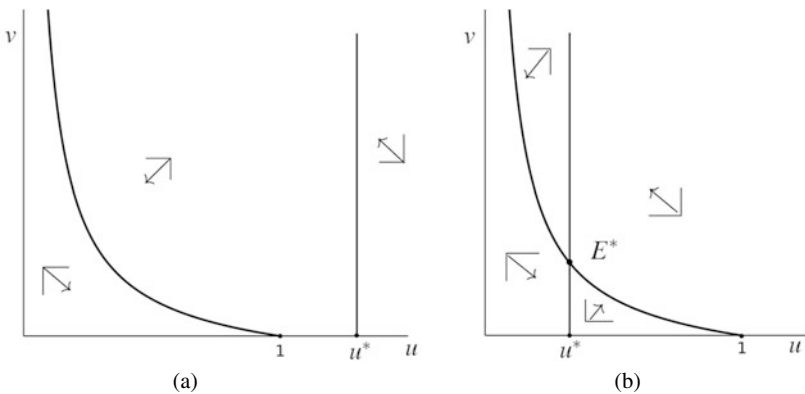


Fig. 6.16 Phase plane for the chemostat model (6.22). The dynamics is similar to that of a predator-prey system (see Problem 6.7): (a) $u^* > 1$, when the bacteria population goes to extinction; (b) $u^* < 1$; E^* is globally attractive and bacteria survive

The analysis of system (6.22) and of the previous statement is left as Problem 6.7 to be solved with the same procedure used in the previous sections.

In the special case of $\tilde{\mu} = 0$, the asymptotic analysis can be simplified taking advantage of a reduction of system (6.22) to a single non autonomous equation. In fact, summing the two equations in (6.22) we get

$$(u(t) + v(t))' = 1 - (u(t) + v(t)),$$

so that

$$z(t) = 1 - u(t) - v(t) = (1 - u(0) - v(0))e^{-t}. \quad (6.25)$$

Then we can substitute in the second equation getting

$$v'(t) = (h(1 - v(t) - z(t)) - 1)v(t), \quad v(0) \in (0, 1), \quad (6.26)$$

where $\lim_{t \rightarrow +\infty} z(t) = 0$. Now, by a limiting theorem (see Appendix F of [14]) we know that the asymptotic behavior of (6.26) is related to the critical points of the limiting equation

$$v'(t) = (h(1 - v(t)) - 1)v(t). \quad (6.27)$$

These are

$$v_0 = 0, \quad v_1 = \frac{A - B - 1}{A - B} = 1 - u^*$$

that respectively correspond to the two possible outcome (see (6.25))

$$\begin{aligned} i) \quad & \lim_{t \rightarrow +\infty} (u(t), v(t)) = (1, 0), \\ ii) \quad & \lim_{t \rightarrow +\infty} (u(t), v(t)) = (u^*, 1 - u^*). \end{aligned} \quad (6.28)$$

Now, only one of these two options is valid. In fact, if $u^* > 1$ only (6.28)-i is acceptable and, on the other hand, if $u^* < 1$ only (6.28)-ii is possible because for the limiting equation (6.27) the equilibrium $v_0 = 0$ is unstable. Thus the previous statement on the asymptotic behavior of system (6.22) is proved.

6.6 Kolmogorov's framework

The specific models discussed in the previous sections are built adopting specific constitutive form of the basic effect that characterize the dynamics of the interaction between a prey and a predator. The framework provided by Gause type models is sufficiently general; however, in the perspective of a generic model capturing the essential features of the interaction, we may consider the system

$$\begin{cases} H'(t) = F(H(t), P(t))H(t), \\ P'(t) = G(H(t), P(t))P(t), \end{cases} \quad (6.29)$$

where $F(H, P)$ and $G(H, P)$ respectively are the growth rates of the prey and of the predator. They depend on H and P with the following basic assumptions

$$\frac{\partial F}{\partial P} < 0 \quad \text{and} \quad \frac{\partial G}{\partial H} > 0 \quad \text{for} \quad H > 0, \quad P > 0, \quad (6.30)$$

These assumptions characterize system (6.29) as a predator-prey system, since translate into mathematical hypotheses the basic mechanism of the interaction:

an increase of the number of predators produces a decrease of the prey growth rate and, vice-versa, an increase of the number of preys produces an increase of the predator growth rate.

Such a general model, endowed with other generic assumptions on the growth of each species in the absence of the other, has been proposed by Kolmogorov in [7] where general results are shown, supporting the idea that the mechanism above is responsible of possible sustained oscillations.

In the same perspective, a class of models out of the Gause framework, that have received some attention in recent years, is that of ratio-dependent models. The idea in these models is that the functional response of predators does not depend on prey densities, but on the ratio between prey and predator densities, thus we have:

$$\begin{cases} H'(t) = r(H(t))H(t) - \pi \left(\frac{H(t)}{P(t)} \right) P(t) , \\ P'(t) = -\mu P(t) + \omega \left(\frac{H(t)}{P(t)} \right) P(t) . \end{cases}$$

It is not very clear the mechanism why the predation rate of one predator should depend on this ratio. On the other hand, the predictions based on such models, have been deemed by some authors in better agreement with observed data ([1]).

Pushing further the idea that assumptions like (6.30) translate ecological mechanisms, we consider the general two-species system

$$\begin{cases} N_1'(t) = r_1(N_1(t), N_2(t)) N_1(t) , \\ N_2'(t) = r_2(N_1(t), N_2(t)) N_2(t) , \end{cases}$$

and characterize three basic interactions between species through conditions on the growth rates $r_i(N_1, N_2)$. Namely we have:

- species 1 predaes 2: $\frac{\partial r_2}{\partial N_1} < 0, \quad \frac{\partial r_1}{\partial N_2} > 0 ;$
- species 1 and 2 compete: $\frac{\partial r_2}{\partial N_1} < 0, \quad \frac{\partial r_1}{\partial N_2} < 0 ;$
- species 1 and 2 are symbiotic: $\frac{\partial r_2}{\partial N_1} > 0, \quad \frac{\partial r_1}{\partial N_2} > 0 .$

Actually, the symbiotic interaction, also known as *mutualism* has not received much attention because it does not lead to any typical behavior, but the results may strongly depend on specific assumptions.

Concerning competition, this is another basic interaction we will be concerned with in the following chapters.

Problems

6.1. Lotka-Volterra model

Consider Lotka-Volterra model (6.3).

1. Prove estimate (6.8).
2. Given that the trajectory of any solution lies on the closed curve (6.6), use Poincaré-Bendixson theorem to prove periodicity.

6.2. Algal bloom (Modified with permission from [2])

It is often observed that, in the pools where fish have been added, water has a greenish color, indicating a high algal biomass. Try to explain this using a predator-prey system with functional and numerical response of Holling type, assuming that algae (the prey) follow the logistic equation (in absence of predators) and that zooplankton (predators) have mortality rate given by $\mu + bF$ where F is fish density (assumed to be constant). Specifically, find how equilibrium algal biomass varies with fish density F , and comment the results.

6.3. Moose and wolves (Modified with permission from [2])

In all Canada moose are preyed by packs of wolves that cause a relevant mortality. The ecologist Messier has collected data in different areas in the country (see [9]) and found that the following relation (approximately) holds between the density W (# of wolves per km²) of wolves and the density M (# of moose per km²) of moose:

$$W = \frac{0.0587(M - 0.03)}{0.76 + M}.$$

Let us interpret this relation as the isocline of predators, i.e. the equilibrium number of wolves for each constant density M of moose. Is it possible to obtain such an isocline from a predator-prey system of Gause-Rosenzweig-McArthur type?

Messier has also obtained that, in absence of wolves, the growth of moose is logistic with intrinsic rate of growth equal to 0.51 years⁻¹ and carrying capacity equal to 1.96 moose per km², moreover the rate of mortality because of predation (in years⁻¹) is proportional to wolf density and equal to 5.2 W .

Draw the prey and predator isoclines and find the positive equilibrium of the system. Is such equilibrium stable? [Hint: think of the relation between isocline and the differential equation for predators]

6.4. Predation mechanisms

Consider a predator-prey system, in which prey dynamics, in absence of predators, is logistic, while predators interact among themselves. For instance, the number of preys captured per predator could increase with the number of predators (hunting in group could be more efficient) or decrease with the number of predators (predators could waste time fighting among them; or preys may be more careful when there are many predators around).

1. Write a generic system according to these assumptions.
2. Choose a specific model, corresponding to one of those cases.
3. Analyze the equilibria and their stability (local) per the chosen model.

6.5. Leslie predator-prey

Leslie (1948) proposed the following system as a model for the predator-prey dynamics:

$$\frac{dH}{dt} = H(a - bH - cP), \quad \frac{dP}{dt} = P(r - s\frac{P}{H}),$$

in other words, the predators (P) have a logistic type dynamics with carrying capacity proportional to the density of preys (H).

1. State clearly, and in case criticize, the assumptions of the model.
2. Draw the isoclines in the phase plane, and find the positive equilibrium.
3. Show that the function (where (H^*, P^*) is the positive equilibrium)

$$V(H, P) = \log\left(\frac{H}{H^*}\right) + \frac{H^*}{H} + \frac{cH^*}{s} \left(\log\left(\frac{P}{P^*}\right) + \frac{P^*}{P} \right)$$

is a Lyapunov function for the system.

[Hint: the proof requires careful computations: a) compute the derivative along the trajectories of V ; b) using the relations satisfied by H^* and P^* , show that the terms including both H and P cancel, and the derivative is the sum of a term depending only on H and one depending only on P ; c) using again the relations satisfied by H^* and P^* , show that each term is a perfect square, so that the derivative has a definite sign.]

6.6. More on predation mechanisms

Consider the following predator-prey system:

$$\begin{aligned} \frac{dH}{dt} &= H \left[r(1 - H/K) - \frac{\alpha HP}{(H^2 + \beta^2)} \right] \\ \frac{dP}{dt} &= P \left[-c + \frac{\gamma H^2}{(H^2 + \beta^2)} \right] \end{aligned}$$

where all parameters are positive.

1. Give a biological interpretation to these equations.
2. Find all equilibria (in the first quadrant) and study their stability for $\gamma < c$.
3. Assume $\gamma > c$. Find the conditions on K that make unstable the 'equilibrium without predators (but with a positive number of preys).

4. Show that a positive equilibrium (H^*, P^*) , if it exists, is stable if

$$\frac{r}{K} + \alpha P^* \phi'(H^*) > 0$$

where $\phi(H) = \frac{H}{H^2 + \beta^2}$.

[Hint: it is convenient to rewrite the system using the function ϕ , and compute the positive equilibrium and the Jacobian through $\phi(H^*)$ and $\phi'(H^*)$, without explicitly computing these]

5. By simple algebraic steps, show that the condition of stability in (d) is equivalent to

$$1 + \left(\frac{K - H^*}{H^*} \right) \left(\frac{\beta^2 - (H^*)^2}{\beta^2 + (H^*)^2} \right) > 0.$$

6.7. The chemostat

Give details of the analysis of the chemostat model (6.22).

1. Prove well-posedness of the model.
2. Exclude existence of periodic solutions via Dulac criterion.
3. Find equilibria and determine their (global) stability.

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Competition among species

*Un gruppo de formiche,
doppo tanto lavoro,
doppo tante fatiche,
s'ereno fatte la casetta loro
all'ombra der grispigno e de l'ortiche*

.....
*Ècchete che un ber giorno
un Ragno de lì intorno
che viveva in un bucio troppo stretto,
vidde la casa e ce pijò possesso
senza nemmanco chiedeje er permesso.
– Formiche mie, – je disse co' le bone –
quello che sta qui drento è tutto mio:
fateme largo e subito! Er padrone
d'ora in avanti nun sarò che io;
però m'accorderò cor vostro Dio
e ve rispetterò la religgione.¹
Trilussa, "Le formiche e er ragno", 1912*

The *intraspecific competition* mechanism we have introduced in Sect. 1.5 is only one of the aspects of the competitive dynamics within the ecosystem. Actually, the same mechanisms that are responsible for the logistic effect are also active in the competition among different species (*interspecific competition*) and, together with predation, competition is another fundamental ecological interaction. The first of the models we will discuss in this chapter is due to Volterra who presented it in the famous paper [22], in 1926, and provided the mathematical basis for the *exclusion principle* that reads:

two different species cannot indefinitely occupy the same ecological niche, but one of the two necessarily goes extinct, while the other saturates the niche.

This principle is one of the basic principles of Ecology, but has to be balanced with empirical observations showing that inter-specific competition is widespread.

¹ A colony of ants/working hard for a long time/had built their little home/in the shade of a nettle bush ... But on a day .../ a certain spider,/ coming from elsewhere, / where he lived in too much small a hole,/ saw the little house and took it over , /without asking any permission./ – My dear ants, – he softly said,/ – everything here is mine: get out soon!/ Since now on, I will be the only master of this place;/ however I will sign an agreement with your God,/ in order to respect your religion ...

Indeed, other models we will discuss in this chapter show that interspecific competition may actually have more complex outcomes than exclusion; anyway, its typical dynamics is completely different from the dynamics of predation we saw in the previous chapter.

Concerning spiders and ants, they are not exactly competing for the same *ecological niche*, however Trilussa's fable provides a nice metaphor for many relationships within ecology ... and outside.

7.1 Volterra's competition model

We consider two species living in the same habitat and depending on the same resources. Thus they interact because, competing for these resources, they indirectly influence each other. In the language of Ecology the two species are said to have the same *ecological niche*. By this term, in fact, we mean all kind of factors, such as food, space, position etc., on which the life of a species depends. In other words, the growth rate of each species decreases as the abundance of the other increases. Thus a generic model for two species competition is constituted by the system,

$$\begin{cases} N_1'(t) = r_1(N_1(t), N_2(t))N_1(t), \\ N_2'(t) = r_2(N_1(t), N_2(t))N_2(t), \end{cases} \quad (7.1)$$

with the assumption:

$$\frac{\partial r_i}{\partial N_j} < 0, \quad i \neq j, \quad i, j = 1, 2 \quad (7.2)$$

that characterizes competition (see Sect. 6.6).

At the end of the chapter we will return to system (7.1) under assumption (7.2); in this section we consider the specific model proposed by Volterra [22] extending the idea of the logistic model to include the effect of both species. Precisely, he assumed the following forms for the growth rates

$$\begin{aligned} r_1(N_1, N_2) &= r_1 - \gamma_1(h_1N_1 + h_2N_2) \\ r_2(N_1, N_2) &= r_2 - \gamma_2(h_1N_1 + h_2N_2) \end{aligned}$$

where $\gamma_1, h_1, \gamma_2, h_2$ are non negative constants.

Actually, in Volterra's formulation, h_i represents the amount of resource (food) subtracted by one individual of species i so that the term

$$(h_1N_1 + h_2N_2)$$

is a measure of total resource consumption by N_1 individuals of the first species and by N_2 of the second. Moreover γ_i is a measure of the effect that resource depletion produces on species i .

With these premises we have the model proposed by Volterra in 1926

$$\begin{cases} N_1'(t) = (r_1 - \gamma_1(h_1N_1(t) + h_2N_2(t)))N_1(t), \\ N_2'(t) = (r_2 - \gamma_2(h_1N_1(t) + h_2N_2(t)))N_2(t), \end{cases} \quad (7.3)$$

that, in the case one of the species is absent, reduces to a Verhulst equation for the remaining species. If, for instance, $N_1(0) = 0$, then $N_1(t) = 0$ and the equation for $N_2(t)$ reduces to

$$N_2'(t) = (r_2 - \gamma_2 h_2 N_2(t))N_2(t),$$

i.e. to a Verhulst model with intrinsic Malthus parameter r_2 and carrying capacity $K_2 = \frac{r_2}{h_2 \gamma_2}$. Actually

$$K_i = \frac{r_i}{h_i \gamma_i}$$

is the carrying capacity of species i , when isolated.

The first property that needs to be proved is the well-posedness of the problem. The result appears obvious from the biological point of view, but it is a necessary first step in a mathematical argument. We leave to Problem 7.1 the proof of the following fact:

for each initial value $N_1(0) > 0$, $N_2(0) > 0$, there exists a unique solution to system (7.3), defined on $[0, +\infty)$, such that

$$0 < N_1(t) < M_1, \quad 0 < N_2(t) < M_2$$

for appropriate choices of M_1 and M_2 .

We now wish to determine the behavior of the solutions; to this aim, we manipulate eqs. (7.3) in order to eliminate the term $(h_1N_1 + h_2N_2)$. Namely we multiply the first equation by $\gamma_2/N_1(t)$ and the second by $\gamma_1/N_2(t)$ to get

$$\begin{aligned} \frac{\gamma_2}{N_1(t)} N_1'(t) &= r_1 \gamma_2 - \gamma_1 \gamma_2 (h_1 N_1(t) + h_2 N_2(t)), \\ \frac{\gamma_1}{N_2(t)} N_2'(t) &= r_2 \gamma_1 - \gamma_1 \gamma_2 (h_1 N_1(t) + h_2 N_2(t)), \end{aligned}$$

and

$$\frac{d}{dt} (\gamma_1 \ln N_2(t) - \gamma_2 \ln N_1(t)) = r_2 \gamma_1 - r_1 \gamma_2$$

or

$$\frac{d}{dt} \ln \left(\frac{N_2^{\gamma_1}(t)}{N_1^{\gamma_2}(t)} \right) = r_2 \gamma_1 - r_1 \gamma_2.$$

Consequently we have

$$\frac{N_2^{\gamma_1}(t)}{N_1^{\gamma_2}(t)} = \text{cost } e^{(r_2 \gamma_1 - r_1 \gamma_2)t}. \quad (7.4)$$

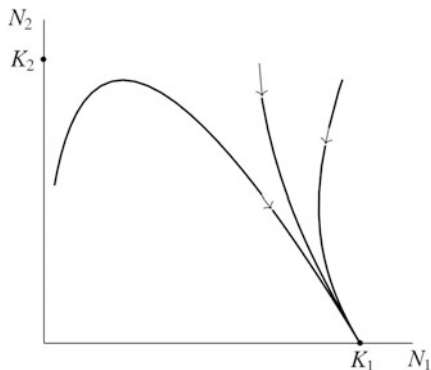


Fig. 7.1 Competitive exclusion in the case $h_2 K_2 < h_1 K_1$. We note a transient behavior showing a possible strong initial increase of $N_2(t)$ before suffering the effect of competition

If

$$r_2 \gamma_1 - r_1 \gamma_2 < 0, \quad (7.5)$$

since $N_1(t)$ is bounded by M_1 , (7.4) yields

$$\lim_{t \rightarrow +\infty} N_2(t) = 0. \quad (7.6)$$

Concerning $N_1(t)$, we note that by (7.6), the first equation in (7.3) can be viewed as a single non-autonomous equation

$$N_1'(t) = (r(t) - \gamma_1 h_1 N_1(t)) N_1(t), \quad (7.7)$$

where

$$\lim_{t \rightarrow +\infty} r(t) = r_1 > 0.$$

Then it is possible to prove (see problem 7.2)

$$\lim_{t \rightarrow +\infty} N_1(t) = K_1 = \frac{r_1}{\gamma_1 h_1}. \quad (7.8)$$

In conclusion we have:

for system (7.3), if $r_2 \gamma_1 - r_1 \gamma_2 < 0$ then

$$\lim_{t \rightarrow +\infty} (N_1(t), N_2(t)) = (K_1, 0). \quad (7.9)$$

By symmetry, we also have

$$\text{if } r_2 \gamma_1 - r_1 \gamma_2 > 0 \text{ then } \lim_{t \rightarrow +\infty} (N_1(t), N_2(t)) = (0, K_2).$$

The behavior of the model is completely determined and does not depend on the initial datum. In Fig. 7.1 different trajectories of the system are shown, for different initial data, in the case of condition (7.5) on the parameters. We note that, although species 2 is doomed to extinction, it is possible that $N_2(t)$ initially increase rapidly before suffering the effect of competition.

The conclusions drawn by the analysis of the model constitute the mathematical basis of the ecological principle of exclusion. Condition (7.5) that was written in terms of intrinsic growth rates and resistance to resource depletion can be also written as

$$h_2 K_2 < h_1 K_1 \quad (7.10)$$

in terms of resource consumption and carrying capacities. In particular, (7.10) shows that species 1 wins the competition because, at its carrying capacity, it depletes the resources more than species 2.

In Chap. 1, Fig. 1.9, we have already shown Gause data relative to separate culture of *Paramecium aurelia* and *Glaucoma scintillans*. Gause also grew the two together, obtaining the results shown in Fig. 7.2 with the eventual exclusion of *Paramecium aurelia*. Instead, *Paramecium aurelia* excluded *Paramecium caudatum*, when grown in co-culture, as shown in Fig. 7.3. These experiments, performed few years after Volterra's theoretical results, lent support to the exclusion principle and its further elaborations.

In the following sections, we discuss how to model specific competition mechanisms, in particular through resource consumption, and whether the same conclusions hold.

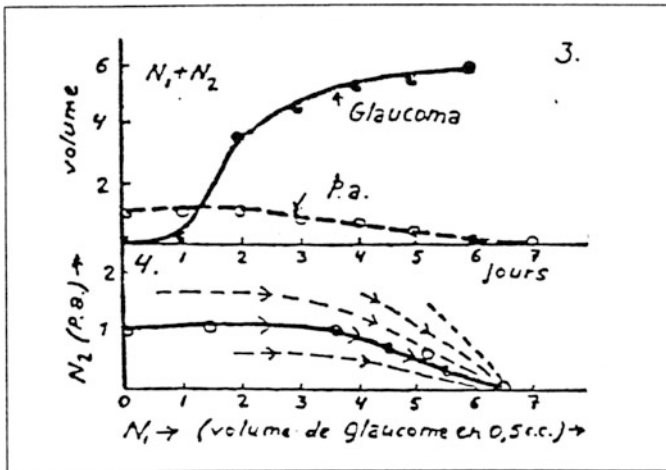


Fig. 7.2 Competition between *Paramecium aurelia* and *Glaucoma scintillans*, ending with exclusion of *Paramecium aurelia*. The upper graph shows data of abundances of the two species as a function of time. In the graph below the same data are shown in the phase-plane (N_1, N_2) . From [6]

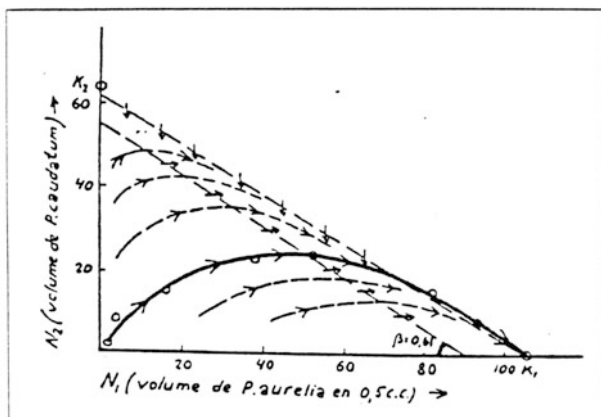


Fig. 7.3 Experimental phase plane dynamics for the competition between *Paramecium aurelia* and *Paramecium caudatum*. Here exclusion of *Paramecium caudatum* occurs. From [6]

The concept of ecological niche and the exclusion principle

The concept of **ecological niche** has attracted the attention of theoretical ecologists for a long time since the first decades of the 20th century, also in connection with the early steps of mathematical population dynamics. In fact, the formal use of the term, though initially introduced by G.S. Elton [4] to generically indicate the habitat features proper to a given species, was initiated by Gause [3] in the discussion of the experimental verification of Lotka-Volterra equations (see later in this chapter).

Around the middle of 20th century, the concept was further developed and formalized by Hutchinson [11, 12] as a region of an n -dimensional space representing the variables of the habitat that have an influence on species growth. This formalization constitutes the key concept of **niche theory**, attempting to provide a description of competition mechanisms to be used in mathematical models. In particular attempting to provide an explanation of certain parameters entering in the model.

The **ecological principle of exclusion**, quoted and formulated at the beginning of this chapter, was also introduced by Gause [5] in his work, as a result arising from the mathematical analysis of simple competition models [16, 22]. The exclusion principle has guided a large area of ecological research, suggesting that, if very similar species can coexist, it is because their niches, though overlapping in part, do not exactly coincide; in this direction, the most famous example was the discovery by the influential ecologist MacArthur [17] of different feeding habits of coexisting similar species of warblers. Thus, in this context the basic question becomes how much niches have to be differentiated to allow for coexistence.

Recent work suggests that coexistence may occur under non-equilibrium conditions (some examples will be sketched in further chapters), stressing the relevance of the temporal and spatial dimensions of the niche.

7.2 Modeling resource availability

Volterra's model presented in the previous section is based on the generic statement that the action of different species on the same habitat has the effect of reducing the growth rate of each species, without trying to give a detailed description of the process. In Volterra's own words the resource is named *food* and the action of the species is denoted *subtraction*.

In order to arrive at a better description of the mechanisms of resource competition, we may note that often a given species is a resource for another one; conversely, we have seen in the chemostat model of Sect. 6.5 that consumption of an inorganic resource can be modeled in the same way as predation. Then we might conclude that competition can be described in terms of predator-prey models (see [15]).

Still, it is convenient keeping a distinction between *dynamic resources* modeled as prey-species, a simple case of which will be considered in Chap. 9, and *static resources* that are instead included in the traditional competition models to be considered in the present chapter. Such a distinction had been proposed in an influential paper by Armstrong and McGehee [1], who used the terms *biotic* for dynamic and *abiotic* for static. The latter can be defined as a resource which is present in the habitat in a fixed quantity; resource uptake by one individual subtracts the corresponding amount from the available resource pool. When an individual dies, the resource that had been taken goes back to the resource pool. Examples of such resources could be *chemical nutrients* that are incorporated into consumers bodies, *feeding or breeding sites*, *hunting territories*, *physical occupation of space* ...

From the viewpoint of the mathematical model a community of n species, each depending on the same k static resources, can be described by a set of n differential equations, relative to species growth, and a set of k algebraic equations describing resources availability; namely by a system such as

$$\begin{cases} N_i'(t) = u_i(\rho_1(t), \dots, \rho_k(t)) N_i(t), & i = 1, \dots, n; \\ \rho_j(t) = v_j(N_1(t), \dots, N_n(t)), & j = 1, \dots, k. \end{cases} \quad (7.11)$$

Here, the functions $u_i(\rho_1, \dots, \rho_k)$ represent the growth rate of species i as a function of available resources and $\rho_j = v_j(N_1, \dots, N_n)$ represent the available amount of the resource j , as a function of species abundances. It is natural to assume that the rates $u_i(\rho_1, \dots, \rho_k)$ are increasing functions with respect to each variable ρ_j , while the resources $\rho_j = v_j(N_1, \dots, N_n)$ are decreasing with respect to the N_i .

Dynamic resources will instead be represented by variables that are dynamically regulated by a set of differential equations. Hence, the differential system as a whole reads

$$\begin{cases} N'_i(t) = u_i(\rho_1(t), \dots, \rho_k(t)) N_i(t), & i = 1, \dots, n; \\ \rho'_j(t) = \delta_j(\rho_1(t), \dots, \rho_k(t), N_1(t), \dots, N_n(t)), & j = 1, \dots, k. \end{cases} \quad (7.12)$$

The predator-prey models, examined in the previous chapter, can be viewed within this framework with $n = k = 1$. Other models of the same type will be analyzed in Chap. 9.

If the dynamics of the resource species is much faster than the dynamics of the consumer species, the case of dynamic resources can be approximated by a system of the form (7.11). A possible justification for reduction of (7.12) to (7.11) relies on a time-scale argument that can be made precise through singular perturbation theory. Intuitively, if the resource dynamics is much faster than the species growth, then, at any time, the resource can be considered always at the equilibrium values, corresponding to the abundances of the species at that time. Namely (7.12) can be approximated by

$$\begin{cases} N'_i(t) = u_i(\rho_1(t), \dots, \rho_k(t)) N_i(t), & i = 1, \dots, n; \\ 0 = \delta_j(\rho_1(t), \dots, \rho_k(t), N_1(t), \dots, N_n(t)), & j = 1, \dots, k; \end{cases}$$

i.e. a system that could be put in the form (7.11).

Furthermore, in Sect. 7.4, we will show that a model of the form (7.11) can be used when resources are inorganic nutrients that flow in and out of the habitat, instead of being fixed quantities. Hence the applications of system (7.11) are not as limited as might have appeared from the modeling assumptions used in its derivation.

7.3 Competition for one static resource

Adopting the framework provided by (7.11), we now consider n species competing for one single static resource. Namely we consider the system

$$\begin{cases} N'_i(t) = u_i(\rho(t)) N_i(t), & i = 1, \dots, n, \\ \rho(t) = v(N_1(t), \dots, N_n(t)), \end{cases} \quad (7.13)$$

under the conditions:

$$\begin{aligned} i) \quad & u'_i(\rho) > 0, \quad u_i(0) < 0, \quad \lim_{\rho \rightarrow +\infty} u_i(\rho) > 0, \\ ii) \quad & \frac{\partial v}{\partial N_i} < 0, \quad v(0, \dots, 0) > 0, \quad \lim_{N_i \rightarrow \infty} v(0, \dots, 0, N_i, 0, \dots, 0) \leq 0. \end{aligned} \quad (7.14)$$

Note that the Volterra model (7.3) can be included in the present framework setting

$$u_i(\rho) = \gamma_i \rho - \mu_i, \quad v(N_1, N_2) = \rho_{\max} - (h_1 N_1 + h_2 N_2), \quad (7.15)$$

with

$$\mu_i = \gamma_i \rho_{\max} - r_i > 0.$$

Namely, ρ_{\max} (chosen adequately large) represents the total amount of resources and μ_i is the death rate of species i when all resources are occupied and no births occur. Thus, system (7.13) with conditions (7.14) generalizes Volterra model by allowing for an arbitrary number n of species, and especially by allowing the functions u_i and v to be nonlinear.

We must comment on assumption (7.14-ii): why do we allow for the limit of v to be negative, while available resources can in reality only be nonnegative? One may note that simple expressions for v_i that arise naturally, like the linear form (7.15), indeed become negative for high values of N_1 and N_2 . The resulting system clearly makes biological sense only in the set where $v \geq 0$, and it can indeed be checked that such biologically meaningful set is invariant. Hence, we allow for v to become negative for large values of N_i , knowing that the system makes sense only in the subset

$$\Omega \equiv \{\mathbf{N} : v(N_1, \dots, N_n) \geq 0\} \quad (7.16)$$

and that outside Ω the system must be a poor approximation of real processes. One should then check (see Problem 7.3) that indeed Ω is invariant. These same considerations will also apply to the case of more than one resource, treated later in this chapter (see assumption (7.32)).

Condition (7.14-i) implies that it exists $\rho_i^* > 0$ such that

$$u_i(\rho_i^*) = 0, \quad (7.17)$$

i.e. for each species there is a critical value ρ_i^* for resource availability, such that below this value the rate is negative.

In order to avoid the trivial case in which some species is not able to grow even when all the resources are available, we assume moreover

$$v(0, \dots, 0) > \rho_i^* \quad i = 1 \dots n. \quad (7.18)$$

Now, it follows from (7.14-ii) that there exists $K_i > 0$ such that

$$v(0, \dots, 0, K_i, 0, \dots, 0) = \rho_i^*, \quad (7.19)$$

i.e., in the absence of all other species, species i attains its own carrying capacity K_i corresponding to the respective critical value of resource availability ρ_i^* .

Indeed, in the absence of all other species, each species follows the equation

$$N_i'(t) = u_i(v(0, \dots, 0, N_i(t), 0, \dots, 0))N_i(t)$$

which, under the assumptions (7.14) is a generalized logistic model with rate

$$\tilde{r}_i(N) = u_i(v(0, \dots, 0, N, 0, \dots, 0)).$$

To proceed, we assume:

$$\rho_1^* < \rho_2^* \leq \rho_3^* \leq \dots \leq \rho_n^*, \quad (7.20)$$

where we have excluded the (non generic) case in which two species share the minimum value of the threshold. Because of (7.20), together with $u_i'(\rho) > 0$ and $u_i(\rho_i^*) = 0$, we have

$$u_i(\rho_1^*) < 0, \quad \text{for } i \neq 1.$$

Concerning equilibria, in addition to the *extinction equilibrium* $E_0 \equiv (0, \dots, 0)$, system (7.13) has all the following *exclusion states*

$$E_i \equiv (0, \dots, 0, K_i, 0, \dots, 0), \quad i = 1, \dots, n.$$

It is theoretically possible that *coexistence states* exist if two species different from species 1 (say i and j) have the same threshold value, i.e. $\rho_i^* = \rho_j^*$. Since we will show that, under the assumption (7.20), species 1 will exclude all the other ones, such cases are not particularly interesting.

Following usual methods, it can be shown that the previous model is well posed and in particular is easy to show (see Problem 7.3) that the set

$$\Omega_M \equiv \Omega \cap \{0 \leq N_i \leq M, \quad i = 1, \dots, n\} \quad (7.21)$$

is invariant if M is large enough, namely if M is such that

$$v(0, \dots, N_i, \dots, 0) < \rho_1^* \quad \text{for } N_i > M, \quad i = 1, \dots, n. \quad (7.22)$$

Thus we also have that for each initial datum $\mathbf{N}^0 \equiv (N_1^0, \dots, N_n^0)$ the ω -limit set $\omega(\mathbf{N}^0)$ is not empty (see Appendix A).

We now proceed with the proof of the main result of this section, namely the proof of *competitive exclusion*. In fact we have:

consider system (7.13) under the assumptions (7.14), (7.18), (7.20); then if $\mathbf{N}^0 \in \Omega$ and $N_1^0 > 0$ we have

$$\lim_{t \rightarrow \infty} N_1(t) = K_1, \quad \lim_{t \rightarrow \infty} N_i(t) = 0, \quad i \geq 2. \quad (7.23)$$

As (7.13) is not a planar system, one cannot take advantage of Poincaré-Bendixson theory in order to prove this result. We thus follow the method by Armstrong and

McGehee [18] and we split Ω into the sets

$$\begin{aligned}\Omega^+ &= \{\mathbf{N} \in \Omega : v(N_1, \dots, N_n) > \rho_1^*\}, \\ \Omega^0 &= \{\mathbf{N} \in \Omega : v(N_1, \dots, N_n) = \rho_1^*\}, \\ \Omega^- &= \{\mathbf{N} \in \Omega : v(N_1, \dots, N_n) < \rho_1^*\}.\end{aligned}$$

Ω^+ is the set corresponding to enough resources to allow at least species 1 to survive, Ω^- is the set corresponding to not enough resources for any species to survive, Ω^0 is the boundary between Ω^+ and Ω^- .

We analyze the behavior of any trajectory $\mathbf{N}(t) \equiv (N_1(t), \dots, N_n(t))^2$, starting in each region through a sequence of steps that end with (7.23).

Step 1. *The set Ω^+ is invariant.*

Let $\mathbf{N}^0 \in \Omega^+$, then $v(N_1^0, \dots, N_n^0) > \rho_1^*$ and, assuming by contradiction, that Ω^+ is not invariant, we have that the first exit time τ is finite

$$\tau = \inf \{t > 0 \mid \mathbf{N}(t) \notin \Omega^+\} < +\infty.$$

Necessarily

$$v(N_1(\tau), \dots, N_n(\tau)) = \rho_1^*$$

and then (using $u_1(\rho_1^*) = 0$)

$$\begin{aligned}\left. \frac{d}{dt} v(N_1(t), \dots, N_n(t)) \right|_{t=\tau} &= \sum_{i=1}^n \frac{\partial v}{\partial N_i}(N_1(\tau), \dots, N_n(\tau)) u_i(\rho_1^*) N_i(\tau) = \\ &= \sum_{i=2}^n \frac{\partial v}{\partial N_i}(N_1(\tau), \dots, N_n(\tau)) u_i(\rho_1^*) N_i(\tau) \geq 0.\end{aligned}$$

This is not possible. In fact if

$$\left. \frac{d}{dt} v(N_1(t), \dots, N_n(t)) \right|_{t=\tau} > 0,$$

then

$$v(N_1(t), \dots, N_n(t)) < \rho_1^*, \text{ for } t \in (\tau - h, \tau)$$

for some $h > 0$ small enough; this would contradict the definition of τ .

On the other hand if

$$\left. \frac{d}{dt} v(N_1(t), \dots, N_n(t)) \right|_{t=\tau} = \sum_{i=2}^n \frac{\partial v}{\partial N_i}(N_1(\tau), \dots, N_n(\tau)) u_i(\rho_1^*) N_i(\tau) = 0,$$

then necessarily $N_i(\tau) = 0$ for all $i > 1$, so that $N_1(\tau) = K_1$, i.e. the trajectory $\mathbf{N}(t)$ would contain the critical point E_1 , against the uniqueness of solutions of ODEs.

² When we need to show the initial datum we will denote the trajectory by $\mathbf{N}(t, \mathbf{N}^0)$.

Step 2. If $\mathbf{N}^0 \in \Omega^0$ and $\mathbf{N}^0 \neq E_1$, then $\mathbf{N}(t) \in \Omega^+$ for all $t > 0$.

Repeating the previous computation, one has

$$\left. \frac{d}{dt} v(N_1(t), \dots, N_n(t)) \right|_{t=0} = \sum_{i=2}^n \frac{\partial v}{\partial N_i} (N_1^0, \dots, N_n^0) u_i(\rho_1^*) N_i^0 > 0,$$

unless $N_i^0 = 0$ for all $i > 1$; but then, since

$$\rho(N_1^0, 0, \dots, 0) = \rho_1^*,$$

we have $N_1^0 = K_1$, i.e. $\mathbf{N}^0 = E_1$, which has been excluded.

Hence $v(N_1(t), \dots, N_n(t)) > \rho_1^*$ (i.e. $\mathbf{N}(t) \in \Omega^+$) for $t \in (0, h)$ for some $h > 0$. Because of **Step 1**, we have $\mathbf{N}(t) \in \Omega^+$ for all $t > 0$.

Step 3. If $\mathbf{N}^0 \in \Omega^+ \cup \Omega^0$ then $\lim_{t \rightarrow +\infty} \mathbf{N}(t) = E_1$.

Let $\mathbf{N}^0 \neq E_1$, otherwise the conclusion would be trivial. Then by **Step 2** we have $\mathbf{N}(t) \in \Omega^+$ for $t > 0$, so that

$$N_1'(t) = u_1(v(N_1(t), \dots, N_n(t))) N_1(t) > u_1(\rho_1^*) N_1(t) = 0.$$

Thus $N_1(t)$ is increasing and

$$\lim_{t \rightarrow +\infty} N_1(t) = N_1^\infty < +\infty, \quad N_1^\infty \geq N_1^0 > 0.$$

Applying the Lyapunov-La Salle theorem (see Appendix A) to the function

$$V(N_1, \dots, N_n) = N_1,$$

we know that any point $\mathbf{Y} \equiv (Y_1, \dots, Y_n) \in \omega(\mathbf{N}^0)$ must satisfy

$$Y_1 = N_1^\infty$$

and also

$$\dot{V}(N_1^\infty, Y_2, \dots, Y_n) = u_1(v(N_1^\infty, Y_2, \dots, Y_n)) N_1^\infty = 0, \quad (7.24)$$

hence

$$v(N_1^\infty, Y_2, \dots, Y_n) = \rho_1^*,$$

i.e. $\mathbf{Y} \in \Omega^0$. Thus the invariant set $\omega(\mathbf{N}^0)$ is contained in Ω^0 and since the only invariant subset of Ω^0 is the critical point E_1 (see **Step 2**), we have

$$\omega(\mathbf{N}^0) \equiv \{E_1\}$$

and

$$\lim_{t \rightarrow +\infty} \mathbf{N}(t) = E_1.$$

Step 4. If $\mathbf{N}^0 \in \Omega^-$ and $N_1^0 > 0$, then $\lim_{t \rightarrow +\infty} \mathbf{N}(t) = E_1$.

Let now $\mathbf{N}^0 \in \Omega^-$. Since $v(N_1^0, \dots, N_n^0) < \rho_1^*$, either

$$\text{there exist } \tau > 0 \text{ such that } v(N_1(\tau), \dots, N_n(\tau)) = \rho_1^* \quad (7.25)$$

or

$$v(N_1(t), \dots, N_n(t)) < \rho_1^* \quad \text{for } t > 0. \quad (7.26)$$

In the first case (7.25) we have $\mathbf{N}(\tau) \in \Omega^0$ and the proof follows from **Step 3**.

If, instead, (7.26) occurs, then the solution stays in Ω^- and

$$\frac{d}{dt} v(N_1(t), \dots, N_n(t)) > \sum_{i=1}^n \frac{\partial v}{\partial N_i}(N_1(t), \dots, N_n(t)) u_i(\rho_1^*) N_i(t) > 0,$$

so that $v(N_1(t), \dots, N_n(t))$ converges increasingly

$$\lim_{t \rightarrow +\infty} v(\mathbf{N}(t)) = \rho^\infty \leq \rho_1^*.$$

Moreover, applying Lyapunov-La Salle to the function

$$V(N_1, \dots, N_n) = v(N_1, \dots, N_n),$$

in the region Ω^- , we have that any limit point \mathbf{Y} must satisfy

$$\dot{V}(Y_1, \dots, Y_n) = \sum_{i=1}^n \frac{\partial v}{\partial N_i}(Y) u_i(\rho^\infty) Y_i = 0. \quad (7.27)$$

All terms in (7.27) are nonnegative with $u_i(\rho^\infty) < 0$ for $i > 1$, as $\rho^\infty \leq \rho_1^*$. To have the identity (7.27) it must be

$$Y_2 = \dots = Y_n = 0.$$

Now, it is impossible that also $Y_1 = 0$, because then

$$\rho^\infty = \lim_{t \rightarrow +\infty} v(N_1(t), \dots, N_n(t)) = v(0, \dots, 0) > v(K_1, 0, \dots, 0) = \rho_1^*;$$

then, from (7.27), we see that $u_1(\rho^\infty) = 0$, i.e. $\rho^\infty = \rho_1^*$.

We conclude that any limit point Y must then belong to Ω^0 and, as seen in **Step 3**, it must be $Y = E_1$, i.e. $\lim_{t \rightarrow +\infty} \mathbf{N}(t) = E_1$. Thus (7.23) is proved.

The model just discussed confirms, under more general assumptions, the exclusion principle, borne as a consequence of Volterra model, adopted as a basic principle

of ecology and also extensively discussed and criticized. Summarizing, we have just seen that:

in the context of static resources, it is impossible that more than one species coexist exploiting a single resource; the species that out-competes all the others is the one that survives with the least resources (the most efficient).

Applying the present result to Volterra model as written through (7.15) at the beginning of this section, we obtain

$$\rho_i^* = \frac{\mu_i}{\gamma_i},$$

so that species 1 out-competes species 2 when $\rho_1^* < \rho_2^*$, i.e.

$$r_2 \gamma_1 < r_1 \gamma_2$$

that is condition (7.5).

7.4 Competition in the chemostat

In this section we show how competition for resources among micro-organisms in a chemostat (the system of laboratory and industrial culture considered in Sect. 6.5) can be studied using the method of the previous section. The model is particularly interesting, because, on the one hand, it can lend itself to experimental verification; on the other hand, it represents a simplified model of competition among phytoplankton species in a lake or similar environments.

We consider n species in the same chemostat, all feeding on the same nutrient, so that the dimensionless model (6.22) is extended to the following system:

$$\begin{cases} c'(t) = 1 - c(t) - \sum_{i=1}^n \alpha_i(c(t)) w_i(t), \\ w_i'(t) = (\alpha_i(c(t)) - 1) w_i(t), \quad i = 1, \dots, n. \end{cases} \quad (7.28)$$

Here $c(t)$ and $w_i(t)$ are the (rescaled) variables representing, respectively, nutrient concentration and species abundances. Moreover

$$\alpha_i(x) = \frac{A_i x}{1 + B_i x},$$

where the constants A_i and B_i are defined, for each species, as in (6.23) and satisfy

$$A_i > B_i + 1 \quad \text{for all } i = 1 \dots n. \quad (7.29)$$

Note that we have set $\tilde{\mu}_i = 0$ assuming that the intrinsic mortalities can be disregarded.

We now consider the variable

$$q(t) = 1 - c(t) - \sum_{i=1}^n w_i(t)$$

and note that from (7.28) we get

$$q'(t) = -q(t), \quad \text{so that} \quad \lim_{t \rightarrow +\infty} q(t) = 0.$$

This means that the ω -limit set of any solution is contained in the hyper-plane

$$\left\{ 1 - c - \sum_{i=1}^n w_i = 0 \right\}.$$

It is possible to prove (see Appendix F of [20]) that the asymptotic behavior of solutions can be analyzed restricting (7.28) to this hyper-plane. Hence we substitute

$$c(t) = 1 - \sum_{i=1}^n w_i(t),$$

in the second equations of (7.28) and reduce to consider the system

$$w_i'(t) = \left(\alpha_i \left(1 - \sum_{i=1}^n w_i(t) \right) - 1 \right) w_i(t), \quad i = 1, \dots, n. \quad (7.30)$$

Now, if we define

$$\begin{cases} u_i(\rho) = \alpha_i(\rho) - 1 \\ v(w_1, \dots, w_n) = 1 - \sum_{i=1}^n w_i \end{cases}$$

system (7.30) is in the form (7.13) and it can be easily checked that, by (7.29), assumptions (7.14) are satisfied; then, we can compute

$$\rho_i^* = \frac{1}{A_i - B_i}, \quad K_i = \frac{A_i - B_i - 1}{A_i - B_i}$$

i.e. the solutions of (7.17) and (7.19).

Applying (7.23), we see that in the chemostat exclusion occurs and the only surviving species is the one corresponding to the minimum value of $\frac{1}{A_i - B_i}$.

Concerning the interest of this model, in connection with the chemostat as an experimental device, we note that the parameters A_i and B_i can be estimated by growing each species in isolation. Then the present model predicts the outcome of competition when the species are grown together,

Indeed, such an experiment was performed by Hansen and Hubbell [7]; they found a very good qualitative agreement between experimental competition outcomes and model prediction, and also a reasonably good quantitative agreement with solutions of system (7.28).

Note finally that the parameters A_i and B_i depend on ϕ and C_0 (see Sect. 6.5); these can be varied by the experimenter to obtain different situations in the culture.

7.5 Two species living on two static resources

We now extend the previous models, allowing for more than one resource type. To keep the models simple enough, we restrict to the case with 2 species and 2 resources of the static type. It would be easy however, extending the ideas to more species and resources; furthermore, we have already seen how the methods used for static resources can sometimes work for dynamic resources as well.

As in (7.11), we assume that the growth rate of each species depends on the available resources, and that the available resources depend on the density of the two species, namely

$$\begin{cases} N_1'(t) = u_1(\rho_1(t), \rho_2(t)) N_1(t), \\ N_2'(t) = u_2(\rho_1(t), \rho_2(t)) N_2(t), \\ \rho_1(t) = v_1(N_1(t), N_2(t)), \\ \rho_2(t) = v_2(N_1(t), N_2(t)), \end{cases} \quad (7.31)$$

where $N_1(t)$ and $N_2(t)$ represent the densities of the two competing species, while $\rho_1(t)$ and $\rho_2(t)$ the concentrations of available resources of the two types. We may also use, when convenient, the vector notation $\mathbf{N} = (N_1, N_2)$.

The mechanism of competition is determined both by the way the rates $u_i(\cdot, \cdot)$ depend on the resources and by the way the resources $v_i(\cdot, \cdot)$ depend by the population abundances. As a general assumption we assume that the growth rates u_i increase with available resources, and that available resources decrease with species densities. Moreover, it is natural to assume that the growth rates are negative if no resources are available, and become positive when a large enough supply of both resources is available. Finally, we assume that a very high density of either species depletes both resources. Mathematically, this translates into ($i, j = 1, 2$):

$$\begin{aligned} i) \quad & \frac{\partial u_i}{\partial \rho_j} > 0, \quad u_i(0, 0) < 0, \\ ii) \quad & \frac{\partial v_i}{\partial N_j} < 0, \quad \lim_{N_1 \rightarrow \infty} v_i(N_1, 0) \leq 0, \quad \lim_{N_2 \rightarrow \infty} v_i(0, N_2) \leq 0, \\ iii) \quad & u_i(v_1(0, 0), v_2(0, 0)) > 0, \end{aligned} \quad (7.32)$$

where, to avoid trivial cases, assumption (7.32-iii) states that the growth rate of both species is positive in absence of resource depletion due to population density.

The above basic assumptions are not sufficient to represent different mechanisms and we have to supply further specifications. In order to discuss different possibilities we consider the resources phase-plane (ρ_1, ρ_2) and start by looking at the null-clines of the rates

$$\mathcal{U}_i = \{(\rho_1, \rho_2) : u_i(\rho_1, \rho_2) = 0\}.$$

Indeed, assumption (7.32) implies that \mathcal{U}_i is not empty, and can be represented as the graph of a function of ρ_1 or ρ_2 . The shape of these curves is somewhat different according to whether the resources are *substitutable* or *complementary*, following the classification by Leon and Tumpson [13]. In the latter case, availability of *both* resources is essential for population growth, as would be the case for different inorganic nutrients; mathematically this translates into:

$$u_i(0, x) < 0 \quad \text{and} \quad u_i(x, 0) < 0, \quad \text{for } i = 1, 2 \quad \text{and any } x > 0.$$

An extreme case of complementary resources follows *Liebig's minimum law*, corresponding to the following rates

$$u_i(\rho_1, \rho_2) = \min\{u_{i1}(\rho_1), u_{i2}(\rho_2)\} \quad (7.33)$$

where $u_{ij}(\cdot)$ are functions of a single nutrient that satisfy assumptions (7.14) of Sect. 7.3. Examples of possible null-clines in the case of complementary resources are shown in Fig. 7.4. As a technical remark, expression (7.33) does not satisfy assumption (7.32-*i*), as the functions are not differentiable at some points and not strictly increasing. However all the following proofs can be adapted to deal with these peculiarities: this is left to the interested reader.

On the other hand, in the case of substitutable resources (such as different carbon sources), growth rates can be positive also in absence of one resource, i.e. $u_i(\rho_1, 0)$ and $u_i(0, \rho_2)$ become positive for $i = 1, 2$ and ρ_1 and ρ_2 large enough. Resources are *perfectly substitutable* if each can be substituted by an adequate proportion of the other. An example for such a case are the linear rates

$$u_i(\rho_1, \rho_2) = c_{i1}\rho_1 + c_{i2}\rho_2 - d_i, \quad (7.34)$$

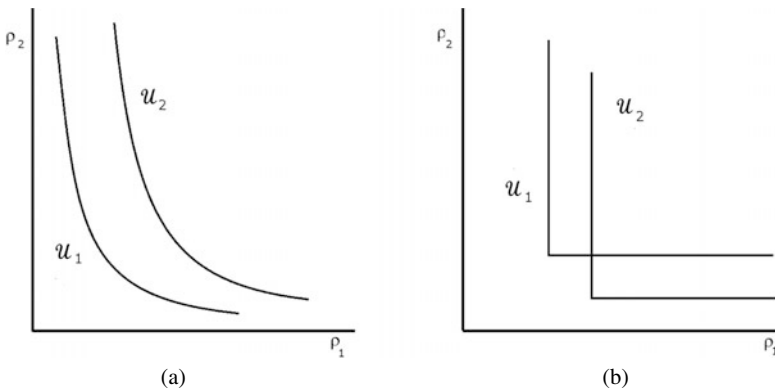


Fig. 7.4 Examples of null-clines for complementary resources. (a) a generic case; (b) the case of Liebig's minimum law. In the first case the null-clines do not intersect; in the second they do, but this is only for illustration

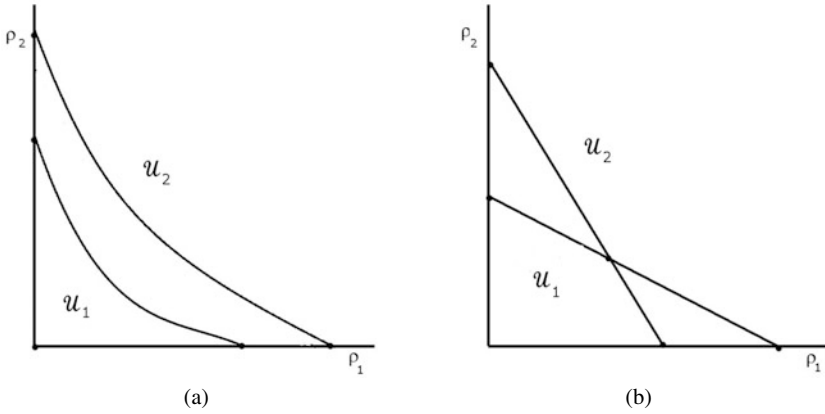


Fig. 7.5 Examples of null-clines for substitutable resources. (a) a generic case; (b) the case of perfectly substitutable resources (see (7.34)). In the first case the null-clines do not intersect; in the second they do, but this is only for illustration

where the null-clines are straight lines. If resources are *partially substitutable*, with the absence of one resource a more than proportional amount of the other will be required to allow for growth. Examples of possible null-clines in the case of substitutable resources are shown in Fig. 7.5.

Possible equilibria of system (7.31) are related to the null-clines \mathcal{U}_i because they may occur at points (ρ_1^*, ρ_2^*) such that

- $u_1(\rho_1^*, \rho_2^*) = 0$ for an equilibrium excluding species 2;
- $u_2(\rho_1^*, \rho_2^*) = 0$ for an equilibrium excluding species 1;
- $u_1(\rho_1^*, \rho_2^*) = u_2(\rho_1^*, \rho_2^*) = 0$ for a coexistence equilibrium.

In the next section we will see that exclusion equilibria always exist while for the existence of a coexistence one it is obviously necessary that the null-clines \mathcal{U}_i intersect (as in the examples of Figs. 7.4 and 7.5) and that the system

$$\begin{cases} v_1(N_1, N_2) = \rho_1^* \\ v_2(N_1, N_2) = \rho_2^* \end{cases}$$

has a solution.

When Liebig's law holds, we can give a precise meaning to the concept of *limiting resource*. In fact, if the intersection point lies in the horizontal side of \mathcal{U}_1 (as in Fig. 7.4-(b)), this means that, if we added or subtracted from the system a small amount of resource 1, the point would still remain on the \mathcal{U}_1 , and there would be no growth or decrease of the population. On the other hand, if we increase resource 2, we would move in the set where $u_1(\rho_1, \rho_2) > 0$ and, if we decrease it, the growth rate would become negative. In this sense, we can say that, at the equilibrium, resource 2 is limiting for species 1, while resource 1 is not limiting (it is still an essential re-

source, though). Conversely, in the same example of Fig. 7.4, since the intersection point lies in the vertical side of \mathcal{U}_2 , resource 1 is limiting for species 2, while resource 1 is not.

7.6 General aspects of two species dynamics

The discussion above focuses on the dependence of the rates on resource availability. We have to complete the framework with the modeling of how resources are consumed by the two species, namely with the two functions $v_1(N_1, N_2)$ and $v_2(N_1, N_2)$. In fact the dynamics of the populations in connection with the different mechanisms represented above is determined by the rates

$$r_i(N_1, N_2) = u_i(v_1(N_1, N_2), v_2(N_1, N_2)), \quad (7.35)$$

leading to the corresponding specific two-dimensional ODE system on the variables $N_1(t)$ and $N_2(t)$

$$\begin{cases} N_1'(t) = r_1(N_1(t), N_2(t)) N_1(t), \\ N_2'(t) = r_2(N_1(t), N_2(t)) N_2(t). \end{cases} \quad (7.36)$$

By (7.32) the rates (7.35) satisfy the basic assumption (7.2) regulating *interspecific* competition, but we also have

$$\frac{\partial r_i}{\partial N_i} < 0, \quad i = 1, 2 \quad (7.37)$$

i.e. each species undergoes also *intraspecific* competition.

The dynamics of the two species is represented in the phase-plane (N_1, N_2) , where as usual we investigate existence of equilibria. There exist the extinction equilibrium $E_0 = (0, 0)$ and the two exclusion equilibria

$$E_1 = (K_1, 0), \quad E_2 = (0, K_2) \quad (7.38)$$

where K_1 and K_2 respectively satisfy

$$r_1(K_1, 0) = 0, \quad r_2(0, K_2) = 0. \quad (7.39)$$

In fact, if we consider the functions

$$\tilde{r}_1(N) = r_1(N, 0) \quad \text{and} \quad \tilde{r}_2(N) = r_2(0, N), \quad (7.40)$$

it is immediate to see from (7.32) (in particular by (7.37)) that

$$\tilde{r}'_i(N) < 0, \quad \tilde{r}_i(0) > 0, \quad \lim_{N \rightarrow \infty} \tilde{r}_i(N) < 0,$$

so that there exist unique K_i such that $\tilde{r}_i(K_i) = 0$, ($i = 1, 2$). Actually $\tilde{r}_i(N)$ is the growth rate of species i , in the absence of the competitor, thus K_i represents the carrying capacity for species i , and correspondingly we have the exclusion equilibria (7.38).

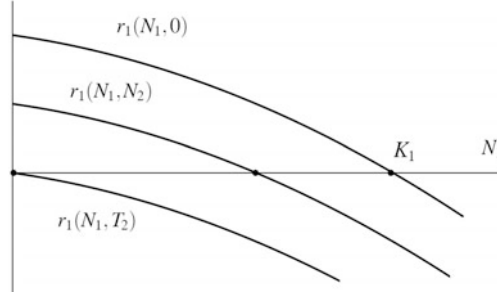


Fig. 7.6 The growth rate of species 1 for different values of the abundance of species 2. The growth rate decreases with N_2 and it is negative for $N_2 \geq T_2$

With the same argument used to determine the carrying capacities K_i , it can be proved the existence of the values T_i that satisfy

$$r_1(0, T_2) = 0, \quad r_2(T_1, 0) = 0. \quad (7.41)$$

The meaning of these parameters is that T_i is a threshold value. Namely, if the abundance of species i is above T_i , then its competitor j has a negative growth rate at any $N_j > 0$ (see Fig. 7.6 for a graphical explanation).

The isocline curves

$$\mathcal{R}_i = \{(N_1, N_2) : r_i(N_1, N_2) = 0\}, \quad i = 1, 2, \quad (7.42)$$

divide the phase plane (N_1, N_2) into regions where the rates are positive or negatives and also give information on existence of coexistence states.

Indeed, the two descriptions in the phase-planes (ρ_1, ρ_2) and (N_1, N_2) are deeply connected through the transform

$$\mathcal{V}(\mathbf{N}) \equiv (v_1(N_1, N_2), v_2(N_1, N_2)),$$

that, as it occurs in most models, we assume to be *invertible*. This assumption, in fact, allows to draw topologically equivalent pictures in the two phase planes.

In Fig. 7.7 we present a particular example (to be analyzed in the next section) to show how $\mathcal{V}(\cdot)$ transforms the plane (N_1, N_2) into the plane (ρ_1, ρ_2) . In fact in Fig. 7.7-(a) the curves

$$\mathcal{C}_1 = \{(v_1(s, 0), v_2(s, 0)), s \geq 0\}, \quad \mathcal{C}_2 = \{(v_1(0, s), v_2(0, s)), s \geq 0\}, \quad (7.43)$$

are the images of the coordinate axes in (N_1, N_2) and represent the resources that would be available with only one species present.

Note that both curves are oriented as the parameter s increases from 0 to $+\infty$; they start at the point $\mathcal{V}(E_0) \equiv (v_1(0, 0), v_2(0, 0))$ and intersect the coordinate axis when either $v_1(N_1, N_2)$ or $v_2(N_1, N_2)$ become negative. Actually, the image $\mathcal{V}(\Omega)$ will be the wedge enclosed by the two curves, that is the feasible region in the plane (ρ_1, ρ_2) . It depends on the functions $v_i(N_1, N_2)$, i.e. on the way the two species consume the

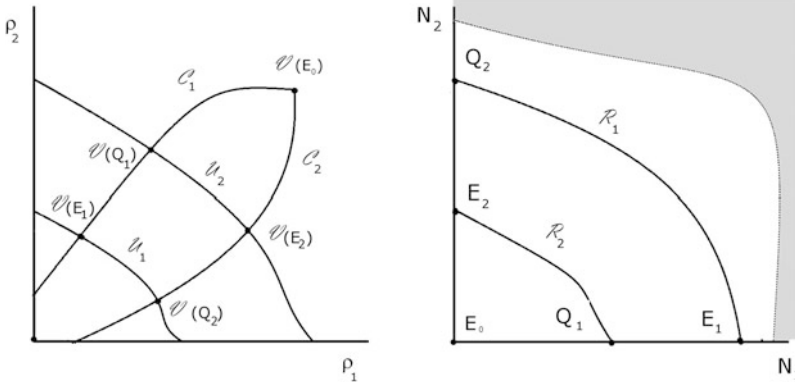


Fig. 7.7 An example showing the correspondence between the phase-plane (N_1, N_2) and the phase-plane (ρ_1, ρ_2) . The gray zone correspond to the non realistic region where at least one of the functions $v_i(N_1, N_2)$ is negative. The curve \mathcal{C}_1 first crosses \mathcal{U}_2 and after \mathcal{U}_1 , thus the point $\mathcal{V}(Q_1)$ precedes $\mathcal{V}(E_1)$ and in the plane (N_1, N_2) the point Q_1 precedes the point E_1 on the coordinate axis $N_2 = 0$ ($T_1 < K_1$). This example shows the case of a globally more efficient competitor (species 1) to be analyzed in Sect. 7.7

resources. Furthermore the curves \mathcal{U}_i are the images of the isoclines \mathcal{R}_i and cross the curves \mathcal{C}_i at the images of the points E_i and Q_i , in the order determined by the values of T_i and K_i . Namely, on the curve \mathcal{C}_i , we have

$$\mathcal{V}(Q_i) \text{ precedes } \mathcal{V}(E_i) \text{ if and only if } T_i < K_i. \quad (7.44)$$

Finally, in the plane (ρ_1, ρ_2) , the intersecting curves identify significant regions that correspond to the regions of the plane (N_1, N_2) where the rates have different signs.

The qualitative picture in the phase plane (ρ_1, ρ_2) allows also to determine the stability of the exclusion equilibria E_1 and E_2 . In fact, at these points the respective Jacobian of system (7.36) read

$$J[E_1] = \begin{pmatrix} K_1 \frac{\partial r_1}{\partial N_1}(K_1, 0) & K_1 \frac{\partial r_1}{\partial N_2}(K_1, 0) \\ 0 & r_2(K_1, 0) \end{pmatrix},$$

$$J[E_2] = \begin{pmatrix} r_1(0, K_2) & 0 \\ K_2 \frac{\partial r_2}{\partial N_1}(0, K_2) & K_2 \frac{\partial r_2}{\partial N_2}(0, K_2) \end{pmatrix}.$$

Thus E_1 is asymptotically stable if

$$r_2(K_1, 0) < r_2(T_1, 0) = 0$$

i.e. if $T_1 < K_1$ because of (7.37). Similarly, E_2 is asymptotically stable if $T_2 < K_2$. Equivalently (see (7.44)), we can say that E_i is asymptotically stable, if on the curve \mathcal{C}_i , the point $\mathcal{V}(Q_i)$ precedes $\mathcal{V}(E_i)$.

Concerning other equilibria, it is clear that a coexistence equilibrium E^* may exist only at a resource level $\mathcal{V}(E^*)$ where the two null-clines \mathcal{U}_1 and \mathcal{U}_2 intersect. However, in order to have a coexistence equilibrium it is not enough the two curves \mathcal{U}_i intersect because this intersection must occur in the feasibility region enclosed by the curves \mathcal{C}_i , i.e. it depends on the functions $v_i(N_1, N_2)$.

In the next section, we will examine the case where the two null-clines do not intersect and in the following one, the case where they do intersect. In principle, assumption (7.32-i) allows for an arbitrarily large number of points in which the two null-clines intersect; however, not being aware of general biological motivations for multiple intersections, we will restrict, for the sake of simplicity, to the case with a single intersection.

7.7 The case of a globally more efficient competitor

We consider here the case, where the null-clines \mathcal{U}_1 and \mathcal{U}_2 do not intersect, and (without loss of generality) the case of species 1 being able to survive with fewer resources than species 2. This case is represented in Fig. 7.7 and, since the lines do not cross, there are, as discussed above, no coexistence equilibria. Thus we are left with the extinction equilibrium E_0 and with the exclusion equilibria E_1 and E_2 . Actually, we will show that under such circumstances competitive exclusion occurs, as in the case of several species competing for one resource.

Now, E_0 is completely unstable because its Jacobian reads

$$J[E_0] = \begin{pmatrix} r_1(0,0) & 0 \\ 0 & r_2(0,0) \end{pmatrix},$$

and $r_i(0,0) > 0$. Moreover, because of the relative location of the curves \mathcal{U}_1 and \mathcal{U}_2 we have that the curves \mathcal{C}_i cross first \mathcal{U}_2 and after \mathcal{U}_1 so that the point $\mathcal{V}(Q_1)$ precedes $\mathcal{V}(E_1)$ while $\mathcal{V}(E_2)$ precedes $\mathcal{V}(Q_2)$. As a consequence E_1 is asymptotically stable, while E_2 is a saddle point.

Passing to the phase plane (N_1, N_2) , this scenario allows to conclude that E_1 is indeed globally attractive, in fact since there exist no periodic solution (there are no equilibria in the positive quadrant), an application of Poincaré-Bendixson Theorem implies that the ω -limit set of any trajectory must be an equilibrium, and the only asymptotically stable equilibrium is actually E_1 .

In conclusion we have indeed again an exclusion result:

in a two species competition for two resources, if one species is globally more efficient than the other (i.e. is able to maintain itself at a lower level of both resources), then there are no coexistence equilibria and the more efficient species out-competes the other one.

It is possible to extend this result to the case on n competitors and also k resources, following the method used in Sect. 7.3 (see Problem 7.4).

7.8 Possible coexistence of two competitors

In the previous section we have analyzed the case when the curves \mathcal{U}_i do not intersect and consequently no coexistence equilibrium can exist. We now explore the case when they intersect and, as stated above, we limit ourselves to the case where they intersect exactly once at a point $\mathbf{r}^* \equiv (\rho_1^*, \rho_2^*)$. There are then four possible cases, shown on the left panels of Figs. 7.8–7.11:

- i) \mathcal{C}_1 and \mathcal{C}_2 cross \mathcal{U}_1 and \mathcal{U}_2 on the same side of the intersection point \mathbf{r}^* ; moving along \mathcal{C}_i from $\mathcal{V}(E_0)$, the curve \mathcal{U}_2 is encountered before \mathcal{U}_1 ,
- ii) \mathcal{C}_1 and \mathcal{C}_2 cross \mathcal{U}_1 and \mathcal{U}_2 on the same side of the intersection point \mathbf{r}^* ; moving along \mathcal{C}_i from $\mathcal{V}(E_0)$, the curve \mathcal{U}_1 is encountered before \mathcal{U}_2 ,
- iii) \mathcal{C}_1 and \mathcal{C}_2 cross \mathcal{U}_1 and \mathcal{U}_2 on opposite sides of the intersection point \mathbf{r}^* ; moving along \mathcal{C}_1 from $\mathcal{V}(E_0)$, the curve \mathcal{U}_1 is encountered before \mathcal{U}_2 , while the opposite happens moving along \mathcal{C}_2 ,
- iv) \mathcal{C}_1 and \mathcal{C}_2 cross \mathcal{U}_1 and \mathcal{U}_2 on opposite sides of the intersection point \mathbf{r}^* ; moving along \mathcal{C}_1 from $\mathcal{V}(E_0)$, the curve \mathcal{U}_2 is encountered before \mathcal{U}_1 , while the opposite happens moving along \mathcal{C}_2 .

The right panels of Figs. 7.8–7.11 show the corresponding phase-plane with the isoclines. We see that in cases (i) and (ii) the position of the curves \mathcal{C}_i does not allow for any coexistence equilibrium because the feasibility region does not contain \mathbf{r}^* . Thus we are left with two situations equivalent to that of a globally more efficient competitor, already treated in the previous section, when we have exclusion. Namely, we can conclude that in case (i) species 1 over-competes species 2, while in case (ii) species 2 over-competes species 1.

Cases (iii) and (iv) allow for a coexistence equilibrium E^* as shown in the right panels of Figs. 7.10 and 7.11, however the nature of the various equilibria is different in the two cases and we have different conclusion about the dynamics.

Consider first case (iii). Here, each \mathcal{C}_i crosses first the corresponding \mathcal{U}_i so that the equilibria E_1 and E_2 are both saddle points, while E_0 is a repeller. On the other hand, looking at the phase plane in the right panel of Fig. 7.10, one sees that the two regions

$$\Omega^{+-} \equiv \{\mathbf{N} \in \Omega \mid r_1(N_1, N_2) > 0, r_2(N_1, N_2) < 0\},$$

$$\Omega^{-+} \equiv \{\mathbf{N} \in \Omega \mid r_1(N_1, N_2) < 0, r_2(N_1, N_2) > 0\},$$

are positively invariant because the vector field of system (7.36), at the border of these regions points inward, so that any trajectory entering Ω^{+-} or Ω^{-+} cannot exit anymore. This implies that no periodic solution exists for the system and, by Poincaré-Bendixson theorem, the equilibrium E^* must be asymptotically stable and a global attractor.

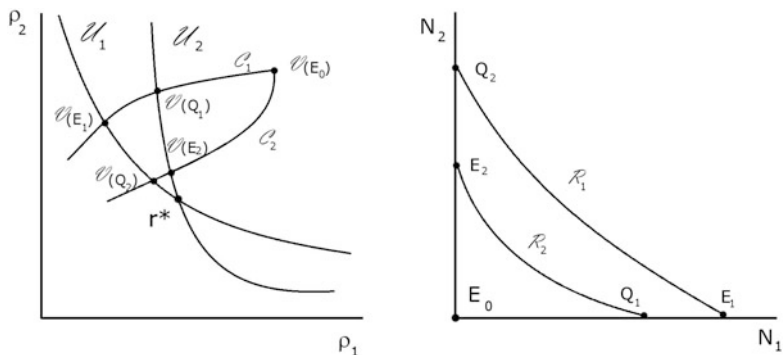


Fig. 7.8 Case *i*. On the left the position of \mathcal{U}_i and \mathcal{C}_j showing that the feasible region does not include the intersection r^* . On the right the corresponding phase plane where the isoclines \mathcal{R}_i do not intersect. In this case, since both \mathcal{C}_1 and \mathcal{C}_2 encounter \mathcal{U}_2 first, we have exclusion in favor of E_1 which is the only asymptotically stable equilibrium and a global attractor

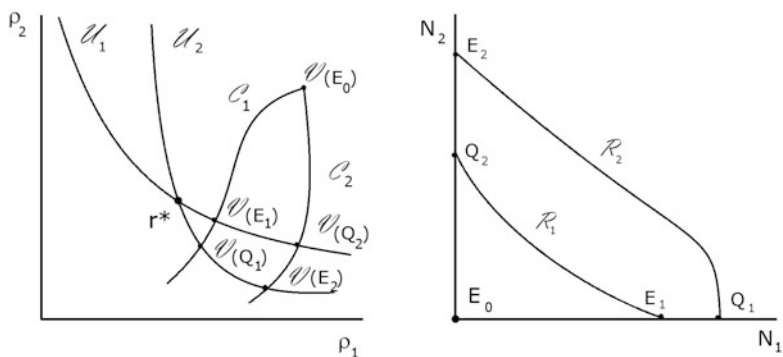


Fig. 7.9 Case *ii*. This case is similar to case *i*, but since both \mathcal{C}_1 and \mathcal{C}_2 encounter \mathcal{U}_1 first, we have exclusion in favor of E_2 which is the only asymptotically stable equilibrium and a global attractor

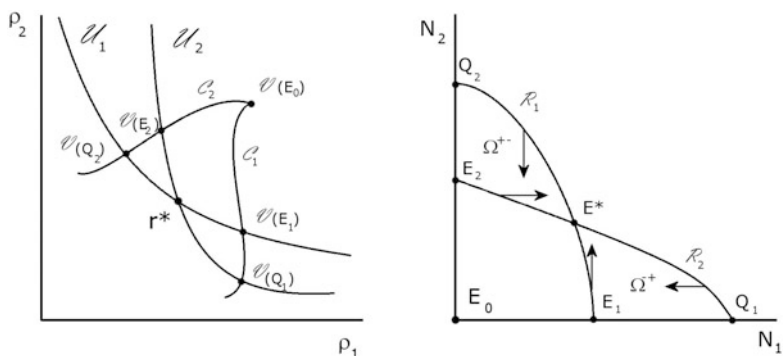


Fig. 7.10 Case *iii*. In the plane (p_1, p_2) the feasible region includes r^* so that in the plane (N_1, N_2) the isoclines \mathcal{R}_i cross and we have a coexistence equilibrium E^* . Since each curve \mathcal{C}_i crosses first the corresponding \mathcal{U}_i both equilibria E_i are unstable. In the picture on the right the field is shown and the invariant regions Ω^{+-} and Ω^{-+} are indicated

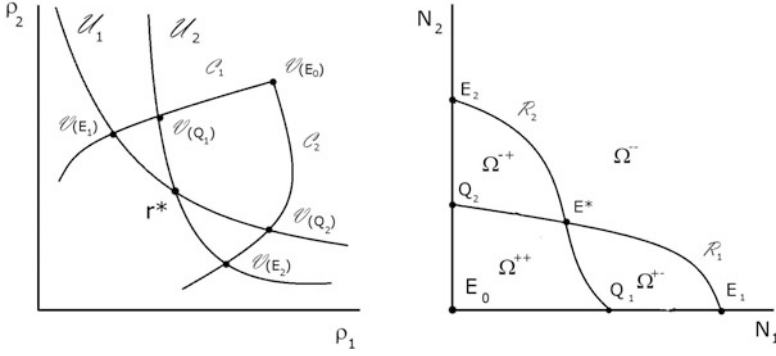


Fig. 7.11 Case *iv*. In this case \mathcal{C}_1 meets first \mathcal{U}_2 and \mathcal{C}_2 meets first \mathcal{U}_1 , then E_1 and E_2 are both asymptotically stable. In the plane (N_1, N_2) the regions Ω^{+-} and Ω^{-+} are still invariant, the coexistence equilibrium E^* is a saddle point and its stable manifold act as a separatrix to determine the attraction basins of E_1 and E_2

We now consider in detail case (*iv*) which is the most complex. In this case E_0 is still a repeller, but both E_1 and E_2 are asymptotically stable. The regions Ω^{+-} and Ω^{-+} are still positively invariant, but in a different position than in the previous case (*iii*) (see the right panel in Fig. 7.11). If, for instance the initial point \mathbf{N}^0 belongs to Ω^{+-} , then $\mathbf{N}(t)$ will belong to Ω^{+-} for all $t \geq 0$ and $N_1(t)$ will be an increasing function, while $N_2(t)$ will be decreasing. Thus $\mathbf{N}(t)$ will converge to the only equilibrium consistent with these features, i.e. E_1 . Analogously, if the initial point \mathbf{N}^0 belongs to Ω^{-+} , $\mathbf{N}(t)$ will converge to E_2 .

Furthermore, we can argue that the coexistence equilibrium E^* is unstable. In fact, solutions starting in any neighborhood of E^* and belonging to Ω^{+-} or Ω^{-+} respectively converge to E_1 or E_2 . Moreover, there must be a separatrix curve between the basins of attraction of E_1 and E_2 , and solutions starting on the separatrix must converge to E^* that hence must be a saddle point.

We also consider the regions

$$\begin{aligned}\Omega^{++} &\equiv \{\mathbf{N} \in \Omega \mid r_1(N_1, N_2) > 0, r_2(N_1, N_2) > 0\}, \\ \Omega^{--} &\equiv \{\mathbf{N} \in \Omega \mid r_1(N_1, N_2) < 0, r_2(N_1, N_2) < 0\}.\end{aligned}$$

Then, if we consider an initial point $\mathbf{N}^0 \in \Omega^{++}$, the trajectory may have different possible behavior. If $\mathbf{N}(t) \in \Omega^{++}$ for all $t \geq 0$, this means that both $N_1(t)$ and $N_2(t)$ are increasing function, so that $\mathbf{N}(t)$ will converge, necessarily to an equilibrium point. Otherwise, there will exist a time $\tau > 0$ such that $\mathbf{N}(\tau)$ is on the boundary of Ω^{++} , i.e. it will be on the boundary between Ω^{++} and Ω^{+-} , or on the boundary between Ω^{++} and Ω^{-+} . In the first case, the solution $\mathbf{N}(t)$ will enter Ω^{+-} for $t > \tau$ and follow the fate of the trajectories starting in Ω^{+-} , i.e. it will converge to E_1 ; in the latter, the solution $\mathbf{N}(t)$ will enter Ω^{-+} for $t > \tau$ and will converge to E_2 .

The case of an initial point $\mathbf{N}^0 \in \Omega^{--}$ is completely analogous to the case of Ω^{++} , except that initially both $N_1(t)$ and $N_2(t)$ will be decreasing functions.

We summarize below all the possible outcome of the competition described by model (7.31), under the assumptions (7.32), in the case when the curves \mathcal{W}_i intersect exactly once. Actually, corresponding to the four possible cases (i) – (iv), respectively illustrated in Figs. 7.8–7.11, we have:

- **case (i)** ($K_1 < T_1, K_2 > T_2$)
there exists no coexistence equilibria and all solutions with $N_1(0) > 0$ converge to the equilibrium E_1 ;
- **case (ii)** ($K_1 > T_1, K_2 < T_2$)
there exists no coexistence equilibria and all solutions with $N_2(0) > 0$ converge to the equilibrium E_2 ;
- **case (iii)** ($K_1 < T_1, K_2 < T_2$)
there exists a unique coexistence equilibrium E^* and all solutions with $N_1(0) > 0$ and $N_2(0) > 0$ converge to the equilibrium E^* ;
- **case (iv)** ($K_1 > T_1, K_2 > T_2$)
there exists a unique coexistence equilibrium E^* which is unstable, for almost all initial points $\mathbf{N}(0)$ the solution converges to one of the two equilibria E_1 and E_2 , which equilibrium is attained depends on the initial value, there exists also a one-dimensional curve of initial points $\mathbf{N}(0)$ such that the solutions starting from them converge to the unstable coexistence equilibrium E^* .

Biologically, we have then found that this rather general model for competition for two resources between two species can have different outcomes:

- stable coexistence at equilibrium;
- unconditional exclusion of one species;
- exclusion of one of two species, depending on initial conditions.

The last outcome is known as the *bistable* case of 2-species competition.

The possibility of coexistence depends in some sense on the differential use of the two resources by the two species. The simpler way to express analytically the condition is in the possibility of the other species to increase when each species is at its carrying capacity, i.e.

$$u_2(\mathcal{V}(E_1)) > 0 \quad \text{and} \quad u_1(\mathcal{V}(E_2)) > 0. \quad (7.45)$$

We note that the previous results have been obtained assuming that the function $\mathcal{V}(\mathbf{N})$ has a continuous inverse. This assumption, that in principle may not be satisfied, allows to simplify the scenario and, from the modeling viewpoint is rather natural, since the functions $v_1(N_1, N_2)$ and $v_2(N_1, N_2)$ are usually taken as linear

$$v_i(N_1, N_2) = \rho_i^m - h_{i,1}N_1 - h_{i,2}N_2, \quad (7.46)$$

where the parameters are all non-negative and have the following meaning

- ρ_i^m = maximum amount of resource i ;
- $h_{i,j}$ = amount of resources of type i used by one individual of species j .

In fact, in this case the \mathcal{U}_i are lines and, excluding the unlikely case where they coincide, the map $\mathcal{V}(\mathbf{N})$ is invertible.

Moving to nonlinear maps $\mathcal{V}(\mathbf{N})$, the condition

$$\frac{\partial v_1}{\partial N_1} \frac{\partial v_2}{\partial N_2} - \frac{\partial v_1}{\partial N_2} \frac{\partial v_2}{\partial N_1} \neq 0, \quad \forall (N_1, N_2) \in \mathbb{R}_+^2. \quad (7.47)$$

of local invertibility, can be proved to be sufficient, together with (7.32-ii), for $\mathcal{V}(\mathbf{N})$ to be globally invertible on Ω (see Gale-Nikaido-Inada theorem at page 20 of [19]). Hence, the assumption that $\mathcal{V}(\mathbf{N})$ is invertible, extensively used in all the previous discussion, can be checked through condition (7.47).

A special case that has been widely studied is instead when both $u_i(\rho_1, \rho_2)$ and $v_j(N_1, N_2)$ are linear functions. This case corresponds to the class of Lotka-Volterra models we will present in next section.

7.9 Lotka-Volterra models

Together with the linear form (7.46) for the resource functions $v_i(N_1, N_2)$ one can consider the following constitutive form of the rates

$$u_i(\rho_1, \rho_2) = \gamma_{i,1}\rho_1 + \gamma_{i,2}\rho_2 - \mu_i, \quad (7.48)$$

where the parameters $\gamma_{i,j}, \mu_i$ are non-negative and are defined as

- $\gamma_{i,j}$: increase of the growth rate of species i per unit of resource j (*dimensions* $[t^{-1} \cdot R^{-1}]$);
- μ_i : death rate of species i when there are no available resources (*dimensions* $[t^{-1}]$).

By substituting the expressions (7.46) into (7.48), one arrives at the system

$$\begin{cases} N_1'(t) = r_1 \left(1 - \frac{N_1(t)}{K_1} - \alpha_{12} \frac{N_2(t)}{K_1} \right) N_1(t) \\ N_2'(t) = r_2 \left(1 - \alpha_{21} \frac{N_1(t)}{K_2} - \frac{N_2(t)}{K_2} \right) N_2(t) \end{cases} \quad (7.49)$$

where we have assumed (see (7.32)-iii) that

$$r_i = \gamma_{i,1}\rho_1^m + \gamma_{i,2}\rho_2^m - \mu_i > 0$$

so that K_i are well defined from (7.39). Moreover

$$\alpha_{12} = \frac{K_1}{T_2}, \quad \alpha_{21} = \frac{K_2}{T_1},$$

where T_i are the threshold parameters defined in (7.41).

System (7.49), with this specific parametrization, is known as the *Lotka-Volterra competition model* and parameters have often been interpreted within the context of the niche-theory, since the early times of mathematical Ecology. A cogent interpretation of the equations was given by G.F. Gause in his essay [3] where the meaning of the coefficients α_{ij} is discussed thoroughly. In fact, in the equations, while the constants K_i keep their meaning of carrying capacities of the corresponding species, the coefficient α_{ij} is a measure of the occupation of the niche of species i by one individual of species j . Namely α_{ij} gives *how many individuals of species i are equivalent to one individual of species j* .

The derivation of the equations through (7.46) and (7.48) yields a similar interpretation in terms of resources consumption. However, eqs. (7.49) can be interpreted also in terms of interference competition, including the cost of aggressive interactions.

Note that the case $\alpha_{12} = 1/\alpha_{21}$ corresponds to Volterra's model of the previous section and, as explicitly commented by Gause, the general case includes the case of two species with partially overlapping niches, so that coexistence is possible because each species may resort on resources that are not consumed by the other. The different scenarios that we have already discussed in the section then correspond to the four situations

- i) $\alpha_{12}K_2 < K_1, \alpha_{21}K_1 > K_2$ species 1 out-compete species 2,
 - ii) $\alpha_{12}K_2 > K_1, \alpha_{21}K_1 < K_2$ species 2 out-compete species 1,
 - iii) $\alpha_{12}K_2 < K_1, \alpha_{21}K_1 < K_2$ the two species coexist,
 - iv) $\alpha_{12}K_2 > K_1, \alpha_{21}K_1 > K_2$ exclusion occurs,
- (7.50)

that, independently from the structure in terms of resources, are exhaustive of all possible occurrences and correspond to different relative positions of the isoclines of system (7.49). Namely, the four conditions listed in (7.50) are respectively equivalent to cases (i)–(iv) discussed in Figs. 7.8–7.11, but here the different occurrences can be interpreted in terms of niche occupancy. In fact in case (7.50)-i we have that when species 2 has reached its carrying capacity, it does not occupy the whole niche of species 1, and instead species 1 over-occupy the niche of species 2; thus the outcome of the competition is exclusion in favor of species 1. In case (7.50)-ii we have

the same situation with the role of the two species exchanged. In case (7.50)-iii each species do not reach the carrying capacity of the other, so that coexistence is possible. Finally, in case (7.50)-iv each species tends to over-compete the other and coexistence is not stable; the outcome in this case is exclusion, depending on the initial abundances of the species.

7.10 General properties of competition models

The several different models for competition that we have considered in the previous section share one typical feature: all solutions converge to an equilibrium, either of coexistence type or with only one species present (exclusion of other competitors). Actually, because of assumptions (7.32), all these models satisfy condition (7.2) that characterizes interspecific competition as in the Kolmogorov framework outlined in Sect. 6.6.

Condition (7.2) ensures that system (7.36) belongs to the class of planar *competitive systems* (see Appendix A) so that any bounded trajectory converges to an equilibrium point. This statement implies in particular that 2-dimensional systems of competitive species *cannot display cycles* of the type we have seen for predator-prey interactions.

We note that a similar situation occurs in the case of systems of *mutualistic* species, also mentioned in Sect. 6.6. In fact this is a kind of dual case and the system falls in the class of planar *cooperative systems* and one can conclude that any solution either goes to infinity or converges to an equilibrium point.

In fact there is not much else to say for mutualistic interaction, unless biological details relative to a specific systems of interacting species are added. This is probably the reason why mutualistic systems have received a limited attention in the theoretical literature.

On the other hand, resource competition is a general theme that can be examined theoretically for generic systems, and shed some light on actual interactions. We have seen that that exclusion necessarily occurs when species compete for one static resource; extending the model to 2 different resources, it is possible that two species then coexist at an equilibrium. Generally, we expect (simply by considering number of equations and number of unknowns) that at most k species will be able to coexist at equilibrium, if they are competing for k resources.

This mathematical property has posed a puzzle to theoretical ecologists for a long time: how can there be so many species on earth given that the number of resources is quite limited? To raise a more precise question: given that algae depend on just a few inorganic limiting resources (nitrogen, phosphorus, and few others) and given that the sea appears to be a rather homogeneous environment, how is it possible to find dozens of phytoplankton species in a barrel of sea water?

An answer could be that coexistence may occur along a periodic cycle, or a more complex trajectory, since the previous results exclude such solutions only for 2-dimensional systems. In fact, in [14] the authors show that $n = 3$ species cannot coexist on $k = 2$ resources, but they cannot exclude coexistence for $n > 3$. The same authors

in [15], after the simulations in [10], indeed prove that $n = 4$ species can coexist on $k = 3$ resources along a periodic solution. In Chap. 9 we will show that, allowing for dynamic resources, 2 predators can coexist on a single prey species (their resource) again along a periodic solution. Thus multi-species interactions may have a richer dynamics than 2-species interactions, and allow more opportunities for coexistence. We will show some instances of possible dynamics in Chap. 9.

Another type of non-equilibrium coexistence concerns the so-called *fugitive species*, species that live in transitory habitats: they are competitively inferior to others, but grow more quickly when resources are abundant and/or reach more quickly a new habitat. This type of interactions are modeled with the so-called *meta-population models* that consider an environment consisting of patches of potential habitats with a small dispersal among them. The prototype model of this type is due to Levins that considered a single species, and used as dynamical variable the fraction of occupied patches (i.e. those patches in which the species is present). This idea has been then extended to predator-prey and competition model, as well as made more realistic in several aspects. A review of these models can be seen in [9].

More generally, the presence of the spatial dimension, even without environmental differences, adds another level of complexity that goes beyond the scope of this text.

Problems

7.1. Model well-posedness-1

Well-posedness of Volterra model (7.3) can be proved showing that the rectangle $\mathcal{R} \equiv \{0 \leq N_1 \leq M_1, \quad 0 \leq N_2 \leq M_2\}$ is invariant, for M_1 and M_2 sufficiently large.

1. Show that on the boundary of \mathcal{R} the differential field of system (7.3) points inward, finding the proper conditions for the constants M_1 and M_2 .
2. Conclude about well-posedness, through the standard Cauchy Theorem.

7.2. Exclusion in Volterra model

In Volterra model, after proving exclusion of species 2 (see (7.6)) we are left with eq. (7.7) and we have to prove (7.8).

1. Choose any $\varepsilon > 0$, find t_0 such that

$$r_1 - \varepsilon \leq r(t) \leq r_1 + \varepsilon, \quad \text{for } t \geq t_0,$$

and solve eq. (7.7), for $t \geq t_0$, as a Bernoulli equation.

2. Prove the estimate

$$\frac{r_1 - \varepsilon}{h_1 \gamma_1} \leq \liminf_{t \rightarrow +\infty} N_1(t) \leq \limsup_{t \rightarrow +\infty} N_1(t) \leq \frac{r_1 + \varepsilon}{h_1 \gamma_1}.$$

3. Conclude showing (7.8).

7.3. Model well-posedness-2

For problem (7.13), together with the usual requirements for well-posedness we need also to show that the set Ω defined in (7.16) is invariant.

1. Prove invariance of Ω showing that the resource $\rho(t) = v(N_1(t), \dots, N_n(t))$ cannot vanish at a finite time, if $\mathbf{N}(0) \in \Omega$.
2. Prove that the bounded set Ω_M defined in (7.21) is invariant with M satisfying (7.22).
3. Conclude about well-posedness, through the standard Cauchy Theorem.

7.4. A globally more efficient competitor for k resources

Show that the result of Sect. 7.7 can be generalized. Consider n species competing for k resources, according to the equations

$$\begin{cases} N'_i(t) = u_i(\rho_1(t), \dots, \rho_k(t))N_i(t), & i = 1 \dots n \\ \rho_j(t) = v_j(N_1(t), \dots, N_n(t)), & j = 1 \dots k \end{cases}$$

with the assumptions (7.32). Assume that species 1 is more efficient in the sense that

$$u_1(\rho_1, \dots, \rho_k) = 0 \implies u_j(\rho_1, \dots, \rho_k) < 0 \quad \forall j = 1 \dots k.$$

Prove that species 1 will outcompete the others.

Hint: follow the structure of the proof in Sect. 7.3, defining

$$\begin{aligned} \Omega^+ &= \{ \mathbf{N} \in \overline{Q} : u_1(v_1(N_1, \dots, N_n), \dots, v_k(N_1, \dots, N_n)) > 0 \}, \\ \Omega^\circ &= \{ \mathbf{N} \in \overline{Q} : u_1(v_1(N_1, \dots, N_n), \dots, v_k(N_1, \dots, N_n)) = 0 \}, \\ \Omega^- &= \{ \mathbf{N} \in \overline{Q} : u_1(v_1(N_1, \dots, N_n), \dots, v_k(N_1, \dots, N_n)) < 0 \}. \end{aligned}$$

7.5. Two species competition

For each of the following systems, determine the outcome of competition:

1.
$$\begin{cases} N'_1 = (60 - 3N_1 - N_2)N_1, \\ N'_2 = (75 - 4N_1 - N_2)N_2; \end{cases}$$
2.
$$\begin{cases} N'_1 = (80 - N_1 - N_2)N_1, \\ N'_2 = (120 - N_1 - 3N_2 - 2N_2^2)N_2. \end{cases}$$

7.6. Time dependent rates

Assume that the dynamics of two competing species can be described by Lotka-Volterra system where the growth rates r_1 and r_2 are periodic functions of t , positive at all times.

1. Find the asymptotic behavior of the system with only one species, say 1.
[Hint: the equation can be solved exactly using the transformation used for obtaining the exact solution of the logistic equation, or via separation of variables. This is actually not necessary, since the asymptotic behavior of N_1 can be guessed intuitively, or obtained by plotting the vector field in the plane (t, N_1)]

2. Find the conditions under which species 2 would increase, if introduced in small numbers when species 1 has approached its asymptotic state. Is it possible to find parameter values such that species 2 would increase, if introduced in small numbers when species 1 is close to its asymptotic state and vice versa?
[Hint: this verbal specification means that a linearization has to be performed],
3. Repeat the scheme assuming that r_1 and r_2 are constant, but the carrying capacities K_1 and K_2 are periodic functions of t (positive at all times). The computations are possible, but awful; it is enough describing the procedure conceptually, after having guessed correctly the asymptotic behavior of the system in the absence of species 2.

7.7. Models and experiments-1 (Modified with permission from [3])

Show that in the Lotka-Volterra competition model, two species can coexist at a stable equilibrium only if the point representing the equilibrium densities of the two species (N_1^*, N_2^*) lies above the line connecting the two equilibria with a single species $(K_1, 0)$ e $(0, K_2)$.

This represents a powerful test of the model: one can grow the two species in isolation, record their equilibrium densities; then grow the two species together and, if they reach a coexistence equilibrium, measure their densities and see whether the condition is satisfied.

Table 7.1 Ayala experiments

	<i>Species grown in isolation</i>	<i>Species grown together</i>
# <i>D. pseudoobscura</i>	664	252
# <i>D. serrata</i>	1251	278

Such an experiment was performed by Ayala with two species of fruit flies, *Drosophila pseudoobscura* and *D. serrata*, obtaining the following results (see [2]):

1. What can we conclude about the competition model?
2. What may be reasons for the discrepancy from theoretical predictions?

7.8. Models and experiments-2 (Modified with permission from [3])

Figure 7.12 shows some results of experiments by Tilman *et al.* (see [21]) with two species of algae (*Asterionella formosa* and *Cyclotella meneghiniana*) in two different circumstances: on the left when phosphates are limiting while silicates are abundant; on the right, when silicates are limiting while phosphates are abundant (see caption for details). Suppose that the two species are grown together in two different experimental set-ups: abundant silicates and limiting phosphates; or abundant phosphates and limiting silicates.

1. Which of the two species will out-compete the other one in the two experiments?
2. Assume that mortality is equal to 0.25 days^{-1} for both species. Moreover, in the experiment with limiting phosphates the concentration of available phosphates P

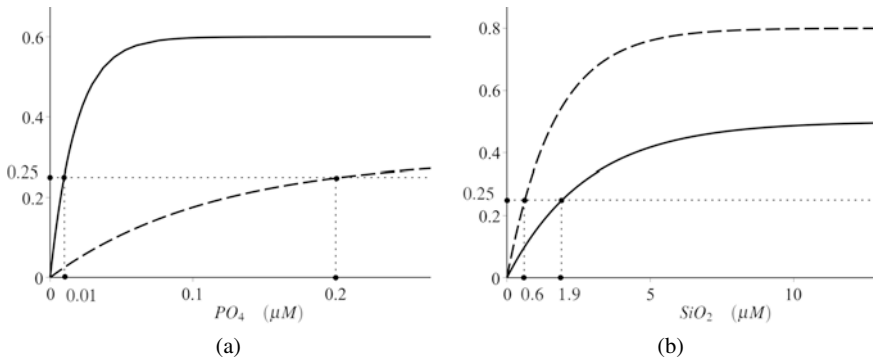


Fig. 7.12 Rates of reproduction (in days⁻¹) of *Asterionella formosa* (continuous line) and *Cyclotella meneghiniana* (dashed line) as a function of PO_4 with abundant silicates (a), or of SiO_2 with abundant phosphates (b)

is obtained from the numbers (per ml) N_1 and N_2 of algae of the two species, according to the following functions

$$P = \frac{2}{1 + 0.02N_1 + 0.01N_2}.$$

Similarly, suppose that in the experiment with limiting silicates the concentration of available silicates S is given by

$$S = \frac{30}{1 + 0.04N_1 + 0.006N_2}.$$

Find the equilibrium concentrations towards which, in the two different experiments, the concentrations of the algae will converge.

- Assume that when a species is grown with limiting both phosphates and silicates, its rate of reproduction is given by the minimum of what shown in the two panels of Fig. 7.12 (Liebig's minimum law). Moreover assume that the available phosphates and silicates are still given by the previous functions, now holding together.

Show that a coexistence equilibrium would then exist, and find its coordinates.

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Mathematical modeling of epidemics

*Haec ratio quondam morborum et mortifer aestus
finibus in Cecropis funestos reddidit agros
vastavitque vias, exhaustit civibus urbem.
nam penitus veniens Aegypti finibus ortus,
aeëra permensus multum camposque natantis,
incubuit tandem populo Pandionis omni.
inde catervatim morbo mortique dabantur.¹
Lucretius, “De Rerum Natura”, Liber VI, 1138–1144*

Epidemics have ever been a great concern of human kind and we are still moved by the dramatic descriptions that arrive to us from the past, as in Lucretius’s sixth book of “De Rerum Natura” or as in other more recent descriptions that we find in the literature. The “Black Death”, the plague that spread across Europe from 1347 to 1352 and made 25 millions of victims, seems to be far from our lives, but more recent events, such as the outbreak of the HIV-AIDS syndrome, remind us that epidemics are an actual problem for health institutions that are continuously facing emerging and reemerging diseases.

Figures 8.1–8.3 display some classical datasets showing typical patterns of epidemic data. Of some infectious diseases (plague, measles, flu) the left panels show a single outbreak, the right panels the occurrence of the disease over several years.

The aim of the mathematical modeling of epidemics is to identify those mechanisms that produce such patterns, to give a rational description of these events and to provide tools for disease control.

In this chapter, the first section is devoted to general concepts and notations; Sect. 8.2 and Sect. 8.3 focus on the deterministic and stochastic models for the single outbreak, Sects. 8.4 and 8.5 on endemic infections. These are the classical models for epidemics description, further sections introduce some extension and more recent developments.

¹ Such was the epidemic, such was the deadly miasma that once fell on the land of Cecrops, making the countryside a scene of death, emptying the streets, and draining the city of citizens. For it originated in the heart of Egypt and, after a long journey through the air and over the floating plains, eventually brooded over the whole people of Pandion. Then they were delivered by thousands to disease and death. (Translation by Martin Ferguson Smith)

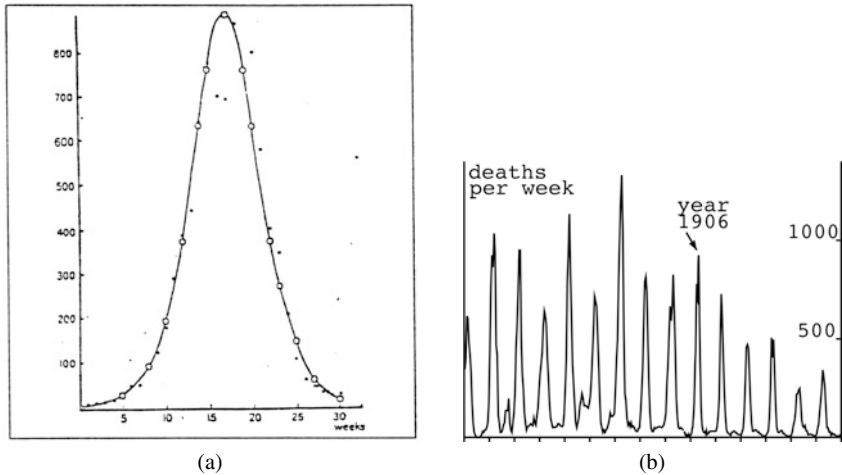


Fig. 8.1 Deaths from plague in Bombay: (a) data from year 1905, together with model fit due to Kermack and McKendrick; (b) data from 1897 to 1911. (a) from [10]; (b) from [2]

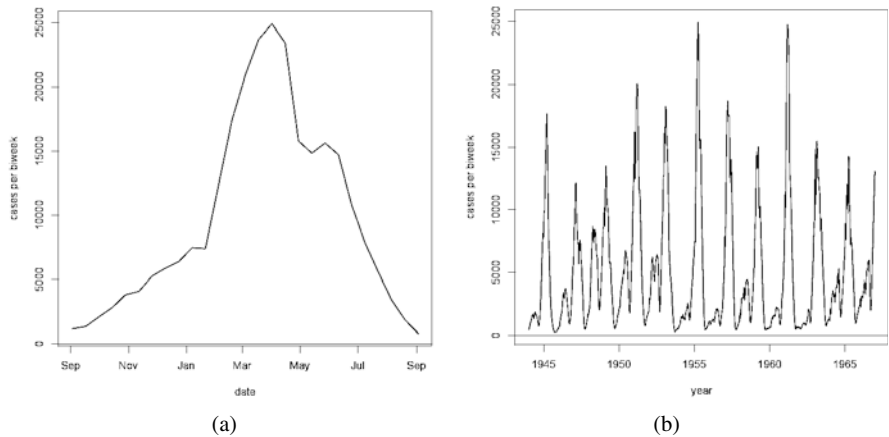


Fig. 8.2 measles epidemics in England: cases reported to health authorities. (a) the single outbreak in 1954–55; (b) data from 1945 to 1966 (start of mass vaccination) showing a roughly biennial pattern

8.1 The basic elements for a description

When considering the spread of an infectious disease within a population, the traditional approach does not focus on the populations of pathogens (bacteria, viruses etc ...), but rather on the number of infected individuals of the host species. In fact, if we are interested in the infection spread at the population level, we may disregard the mechanisms that make the single individual sick; this is justified also because generally the dynamics of pathogen invasion and growth within each individual oc-

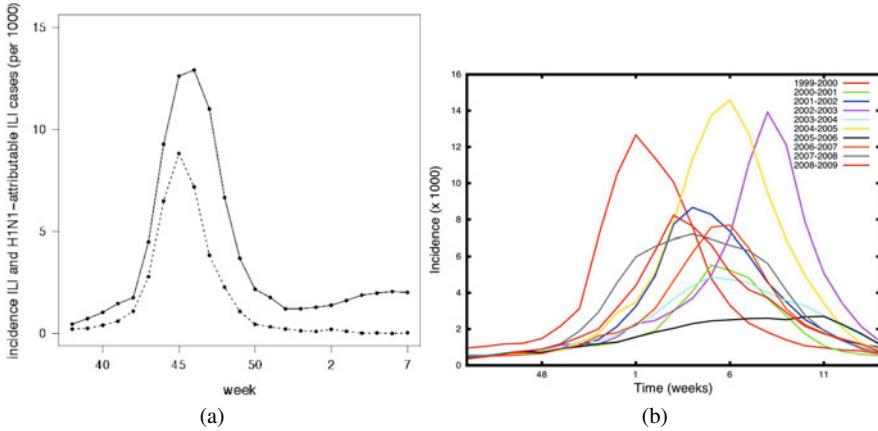


Fig. 8.3 Data reported to the flu surveillance system in Italy. (a) the 2009 pandemic; solid curve displays reported Influenza-Like-Illnesses (ILIs), dashed curve the same cases multiplied by the fraction of examined sampled that tested positive for influenza A virus; (b) weekly ILI cases in all autumn-to-spring seasons from 1999–2000 to 2008–09

curs at a time scale much faster than the timescale of infection transmission from one host to another. Hence the basic elements for the description of epidemics at the *population level* are the three epidemiological classes:

- **Susceptibles**
those individuals who are healthy and can be infected;
- **Infectives**
those individuals who have been infected and are able to transmit the infection;
- **Removed**
those individuals who are immune after having been infected and recovered.

The term *Removed* was introduced by Kermack and McKendrick (whom we owe this framework extensively followed since then) to account not only for individuals that have recovered and are immune, but also for those dead because of the infection, and for those that have been quarantined, after having been identified as infected. At the end of Sect. 8.2 we return to this issue.

On the basis of the previous description, the basic variables identifying the state of the population in the epidemiological perspective are:

- $S(t)$ = the number of susceptibles at time t ;
- $I(t)$ = the number of infectives at time t ;
- $R(t)$ = the number of removed at time t .

Actually, there may be other epidemiological classes characterizing an infection. In fact, for instance, more realistic models take into account a *latency period* occurring between the time an individual is infected and the time she becomes also infectious. In this case, a further class of *exposed* individuals is considered including all the individuals incubating the disease. Also, in some cases it may be necessary to consider different stages of the infection differing in infectiousness. However, considerable insight into the phenomena can be achieved by a description based on the three basic variables $S(t)$, $I(t)$, $R(t)$ introduced above.

After partitioning the population into the epidemiological classes, some assumptions need to be introduced to describe the infection transmission and progression. In this respect, epidemic models are mainly based on the following assumptions:

- susceptibles are infected only after a contact with an infected individual;
- transitions to classes other than the infectives class do not depend on interactions between individuals but are due to infection progression within any individual;
- the population is very large.

Indeed, the last assumption is typical of deterministic population models (see the assumptions of Malthus model in Chap. 1) and could be justified as a limit of a stochastic model. In Sect. 8.3 we present a stochastic model and discuss the similarities and the differences from the deterministic model analyzed in the next section.

Furthermore, a basic distinction may be drawn between those diseases that impart lifelong immunity and those which do not. The first case leads to the so called SIR type models, the second to SIS (no immunity at all) or to SIRS (in case of transitory immunity) models. In fact, in the two cases, the individual paths through the epidemiological classes can be described as in Figs. 8.4, 8.5, 8.6. In these representations, the parameters are defined as:

$\lambda(t)$ = the pro-capita rate at which susceptibles become infected;
 $\gamma(t)$ = the rate at which infectives recover from the disease.

The first parameter $\lambda(t)$, also called *force of infection*, pertains to the infection mechanism which depend on the way people mix and contact other people. It may depend on time either directly, because of seasonal influences, or indirectly because it depends on the size of the epidemiological classes and of the population.

The *removal rate* $\gamma(t)$, instead, depends on the interaction between the pathogen agents and the immune system within an infected individual, and we can assume it is an intrinsic parameter γ . The assumption that the removal rate is constant is a strong one because it amounts to saying that the probability to recover in any given time unit is independent of how long an individual has been infected, in contrast with most empirical knowledge (see Sect. 8.6 for a more structured model). However this

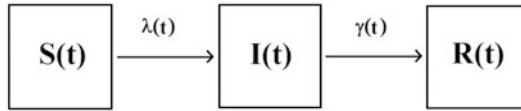


Fig. 8.4 The S-I-R model for diseases which do impart immunity. Susceptible individuals are infected at a rate $\lambda(t)$ and recover at a rate $\gamma(t)$ becoming immune

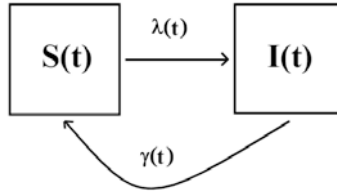


Fig. 8.5 The S-I-S model for diseases which do not impart immunity. The mechanism of infection is the same as in the S-I-R model, but here infected individuals recover becoming again susceptible

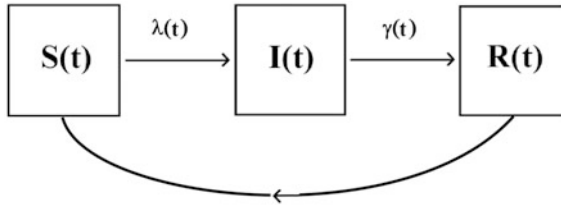


Fig. 8.6 The S-I-R-S model for diseases imparting transitory immunity. The removed individuals become again susceptible

assumption allows for the framework of ordinary differential equations and is then extensively used. Since

$$\Pi(t) = e^{-\gamma t} \quad (8.1)$$

is the probability an individual is still infective after a time t since the infection, the parameter

$$\tau = \frac{1}{\gamma}$$

is the average duration of the infection.

Concerning the force of infection, assuming homogeneous mixing in the population, it can be written as

$$\lambda(t) = c(t) \chi \frac{I(t)}{N(t)}, \quad (8.2)$$

where:

- $c(t)$ = **pro-capita contact rate**
the number of contacts one individual has in the time unit;
- χ = **infectiousness of one contact with an infective**
the probability that a contact produces an infective when one of the two individuals is susceptible and the other is infective;
- $N(t)$ = **total population** = $S(t) + I(t) + R(t)$.

Note that in the previous description we have not defined precisely what we mean by a *contact*. In fact, this will depend on the nature of the infection and on its transmission mechanisms. Thus a *contact* may mean shaking hands, being in the same room, having sexual contacts ... Moreover, the way the contact rate depends on time may be direct (because of seasonal effects) or the contacts may depend on population size and, if the population is changing, consequently on time.

In order to explain the form (8.2) of the force of infection, we compute the number of new infections occurring in a time unit. In fact, following a group of $S(t)$ susceptible individuals, each of them will, on average, contact, in the time unit, $c(t)$ individuals, a fraction $I(t)/N(t)$ of whom will be infective; finally, each contact with infectives will be effective in transmitting the infection with probability χ . As a consequence, choosing a time interval Δt short enough to be able to neglect changes in the epidemiological classes, the number of new infections between t and $t + \Delta t$ will be approximately

$$S(t)c(t)\frac{I(t)}{N(t)}\chi\Delta t, \quad (8.3)$$

from which $\lambda(t)$ is identified.

The form of $\lambda(t)$ rests upon the assumptions that the population is homogeneously mixing, that the whole population is active (instead, for some diseases either part or all of the removed class does not participate in the mixing), that the contact rate is independent of the size of the active population and that contacts with infectives are equally infective.

As a whole, the previous assumptions on the transmission process resemble a sort of *mass action* mechanism (see below a discussion on possible forms of mass action) and the population is considered as a *perfect gas* of particles. Nevertheless, though very simple, this setting allows to set up the basic epidemiological models. These are prototypes that shape all the effort in modeling epidemics.

We end up by mentioning that, beyond the force of infection $\lambda(t)$, other variables of epidemiological interest are:

- **prevalence** $= I(t)/N(t)$
the fraction of infected at time t (a dimensionless number);
- **incidence** $= j(t) = \lambda(t) S(t)$
the number of new infections at time t (dimensions $[N t^{-1}]$).

8.2 The single epidemic outbreak

A single epidemic outbreak (as opposed to disease endemicity) occurs in a time span short enough to neglect demographic changes. Precisely, we assume that no births and deaths occur in the population, either due to normal demographic dynamics or, in this first approach, due to the disease caused by the infection. Moreover, we ignore the incubation period of the disease, and also assume that recovered individuals are permanently immune (we consider a disease of type S-I-R as sketched in Fig. 8.4).

We obtain the following system, involving the three epidemiological classes introduced above

$$\begin{cases} i) & S'(t) = -\lambda(t)S(t), \\ ii) & I'(t) = \lambda(t)S(t) - \gamma I(t), \\ iii) & R'(t) = \gamma I(t), \end{cases} \quad (8.4)$$

with $\lambda(t)$ specified by the constitutive assumption (8.2) with the contact rate c constant.

In fact, according to the dynamics described in Fig. 8.4, eq. (8.4)-i describes the output of susceptibles due to the infection process modeled through (8.2), the new infectives are included in eq. (8.4)-ii where also an output due to recovery is registered and introduced as an input in (8.4)-iii.

System (8.4) has to be completed by initial conditions. We will often assume that $R(0) = 0$, i.e. that at the beginning of the epidemics no individual is immune to the disease (the *pandemic* case). As for the other classes, we will write $S(0) = S_0 > 0$, $I(0) = I_0 > 0$, where generally I_0 is chosen very small to mimic the introduction of a few infected individuals from outside.

The model above was introduced by Kermack and McKendrick (see [10]- [11]) who actually proposed a more general model including the effect of the time elapsed since infection, avoiding the assumption of a constant γ . However in their analysis they specifically consider the particular case of system (8.4) as an important tool for having an insight in the epidemic process.

As the right hand side of (8.4) is Lipschitz (away from $N = 0$), for any positive initial datum, there will be a unique (local) solution. Moreover, adding the three equation in (8.4) we get

$$S'(t) + I'(t) + R'(t) = 0,$$

hence we have that the total population is constant (as implicit in the assumptions)

$$N(t) = S(t) + I(t) + R(t) = S(0) + I(0) + R(0) = N \quad (8.5)$$

and is a parameter of the model, included in the force of infection (8.2) that finally reads

$$\lambda(t) = \frac{\beta}{N} I(t), \quad (8.6)$$

where $\beta = c\chi^2$. Thus system (8.4) becomes

$$\begin{cases} S'(t) = -\frac{\beta}{N} I(t) S(t) \\ I'(t) = \frac{\beta}{N} I(t) S(t) - \gamma I(t) \\ R'(t) = \gamma I(t). \end{cases} \quad (8.7)$$

We note that the first two equations in (8.4) are independent of the value of $R(t)$ so that one can reduce system (8.4) to the first two equations. However we keep all the equations because it is convenient for interpreting the results.

The system can be conveniently scaled with the transformation

$$t \rightarrow \tilde{t} = \gamma t, \quad S \rightarrow u = \frac{S}{N}, \quad I \rightarrow v = \frac{I}{N}, \quad R \rightarrow w = \frac{R}{N}, \quad (8.8)$$

i.e. taking the duration of the disease as time unit and measuring susceptibles, infected and removed as fractions of total population.

We then have, renaming \tilde{t} as t ,

$$\begin{cases} u'(t) = -R_0 u(t) v(t), & u(0) = u_0 \\ v'(t) = R_0 u(t) v(t) - v(t), & v(0) = v_0 \\ w'(t) = v(t), & w(0) = w_0 \end{cases} \quad (8.9)$$

where

$$R_0 = \frac{c\chi}{\gamma} \quad (8.10)$$

is the only parameter left in the equations while, in view of (8.5), the initial conditions u_0 , v_0 and w_0 will satisfy

$$u_0 > 0, \quad v_0 > 0, \quad w_0 \geq 0, \quad u_0 + v_0 + w_0 = 1. \quad (8.11)$$

² We adopt this traditional notation, which of course should not be confused with the traditional way for denoting demographic fertility.

The dimensionless parameter defined in (8.10) is a *basic reproduction number* relative to the epidemics dynamics. Namely we have:

R_0 is the number of secondary cases produced, in a totally susceptible population, by a single infective individual during the time span of the infection.

In fact c represents the average number of individuals contacted by an individual (as a newly infected one) in unit time, and χ is the probability that a susceptible individual, contacted by an infected becomes infected. Thus, assuming everybody else is susceptible, $\beta = c\chi$ is the average number of individuals infected in unit time. Multiplying by the average length of the infectious period $1/\gamma$, one obtains R_0 and its interpretation.

It is not difficult to show that (8.9) has a unique global solution with positive components and any solution satisfies $u(t) + v(t) + w(t) = 1$ (see Problem 8.1). The analysis of the asymptotic behavior of system (8.9) allows a detailed description of the epidemics and explains the role of R_0 (see also [7] and [8]).

From the first equation we have

$$u'(t) < 0 \quad (8.12)$$

so that

$$u(t) \searrow u_\infty \geq 0 \quad \text{as } t \rightarrow \infty. \quad (8.13)$$

On the other hand, from the third equation in (8.9) and using (8.11), we have

$$w_0 + \int_0^t v(s)ds = w(t) = 1 - u(t) - v(t) \leq 1, \quad (8.14)$$

so that

$$\int_0^\infty v(s)ds < +\infty,$$

and, from (8.14),

$$v(t) \rightarrow v_\infty = 1 - u_\infty - \int_0^\infty v(s)ds \leq 1 \quad \text{as } t \rightarrow +\infty.$$

As $v(t)$ converges to a limit, while it is integrable in $(0, +\infty)$, it has to be

$$v(t) \rightarrow 0 \quad \text{as } t \rightarrow +\infty.$$

Thus we have that:

the disease goes to extinction and the number of susceptibles reduces to u_∞ .

Though it is certain that an epidemic will eventually end, its behavior may be qualitatively very different. In fact, the second equation of (8.9)

$$v'(t) = (R_0 u(t) - 1) v(t),$$

together with (8.12) implies that:

- if $R_0 u_0 \leq 1$, then

$$v'(t) < 0 \quad \text{for all } t > 0; \quad (8.15)$$

- if $R_0 u_0 > 1$, then

$$v'(t) > 0 \quad \text{for } t < t^*, \quad \text{and} \quad v'(t) < 0 \quad \text{for } t > t^*, \quad (8.16)$$

where t^* is such that $R_0 u(t^*) = 1$.

The two alternatives are shown in Fig. 8.7 where two solutions corresponding to (8.15) and (8.16) are plotted. Statements (8.15) and (8.16) can be considered a version of the celebrated *threshold theorem* stating that:

a major epidemics occurs if and only if

$$R_0 u_0 > 1. \quad (8.17)$$

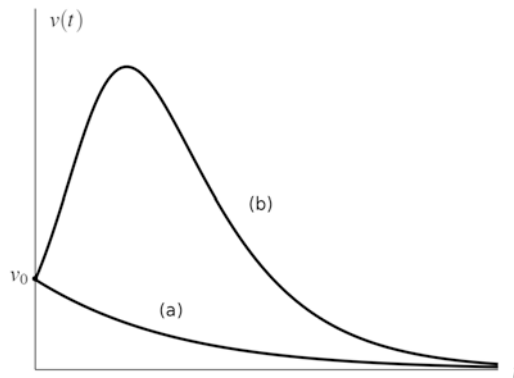


Fig. 8.7 Solutions for problem (8.9) and the threshold condition for an outbreak. (a) here $R_0 u_0 < 1$ and the infective fraction $v(t)$ decreases, no matter what the initial fraction v_0 is; (b) since $R_0 u_0 > 1$ the infective fraction increases before dying out; the maximum prevalence occurs at t^* such that $R_0 u(t^*) = 1$

Condition (8.17) takes into account the initial susceptible fraction u_0 , so that the expected number of individuals infected at the beginning of an epidemic is only $R_0 u_0$, since not everybody is susceptible. Thus condition (8.17) states that in order to have an outbreak, the number of secondary cases from a single infective must be initially greater than 1. We can define the *effective reproduction number* as a dynamic quantity

$$R_e(t) = R_0 u(t)$$

that takes into account the fraction that can be actually infected. In this model, $R_e(t)$ is decreasing as the epidemic goes on and the peak of $v(t)$ is reached at the time t^* such that $R_e(t^*) = 1$. At that time, the susceptible fraction reaches the threshold value

$$u(t^*) = \frac{1}{R_0}, \quad (8.18)$$

below which the infection is not sustained any longer.

We are particularly interested in the final size u_∞ of the susceptible fraction (see (8.13)); indeed $(w_\infty - w_0)$ is the fraction that has been infected during the epidemic course, and can be considered the *size of the epidemic*. As

$$w_\infty - w_0 = 1 - u_\infty - (1 - u_0 - v_0) = u_0 + v_0 - u_\infty \approx u_0 - u_\infty$$

if $v_0 \approx 0$, the epidemic size can be estimated as $u_0 - u_\infty$.

First we note that from the first equation in (8.9) and (8.14) we have

$$u_\infty \geq u_0 e^{-R_0} > 0,$$

meaning that the susceptible class will never be completely depleted at the end of an epidemic.

To have more precise information we note that from the first equation in (8.9) we get

$$u(t) = u_0 e^{-R_0 \int_0^t v(s) ds}$$

and, using (8.14),

$$u(t) = u_0 e^{-R_0(1 - u(t) - v(t) - w_0)}. \quad (8.19)$$

Relation (8.19) provides a first integral for system (8.4) allowing a phase portrait for the (u, v) trajectories as shown in Fig. 8.8. Actually all trajectories are represented by the curves

$$v = \frac{\ln(u)}{R_0} - u + \text{const} \quad (8.20)$$

for different values of the constant which depends on the initial values.

Going to the limit in (8.19) as $t \rightarrow +\infty$, we get the following equation for u_∞

$$u_\infty = u_0 e^{-R_0(1 - u_\infty - w_0)}. \quad (8.21)$$

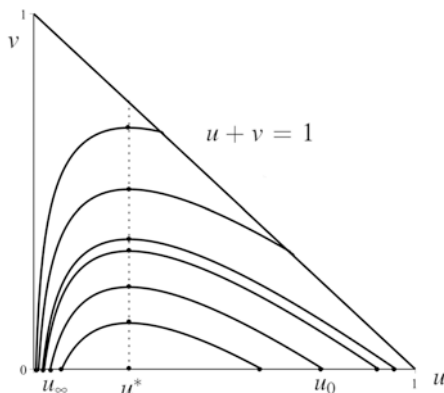


Fig. 8.8 Phase plane for problem (8.9). Different trajectories (8.20) are drawn for the same R_0 and different values of the constant. The feasible region is the triangle delimited by the line $u + v = 1$ and the curves are described from right to left. At the critical value u^* , such that $R_0 u^* = 1$, the infected fraction u starts decreasing. If a solution starts at a point with $u_0 < u^*$, there is no outbreak of the epidemics. Each curve ends on the u axis, at $u = u_\infty$.

Since $u(t)$ is decreasing we have $u_\infty < u_0$ so that u_∞ is determined as a root of the function

$$H(z) := z - u_0 e^{-R_0(1-z-w_0)} \quad (8.22)$$

in the interval $[0, u_0]$.

As $H(0) < 0 < H(u_0)$ and $H''(z) < 0$ for all z , eq. (8.21) has one and only one solution in $(0, u_0)$. In Fig. 8.9 the graph of the function $H(z)$ is plotted in the two cases $R_0 u_0 < 1$ and $R_0 u_0 > 1$. From the picture we have evidence of how the threshold ($R_0 u_0$ above or below 1) affects the size of u_∞ . In fact if $R_0 u_0 < 1$ (case a) then u_∞ is close to u_0 , while if $R_0 u_0 > 1$ (case b) it is close to 0.

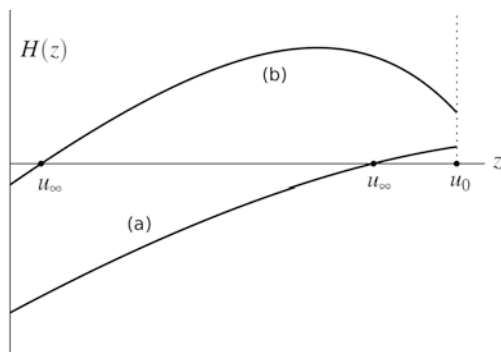


Fig. 8.9 The graph of the function $H(z)$ and the final size of the susceptible fraction, in the two cases $R_0 < 1$ (a) and $R_0 > 1$ (b)

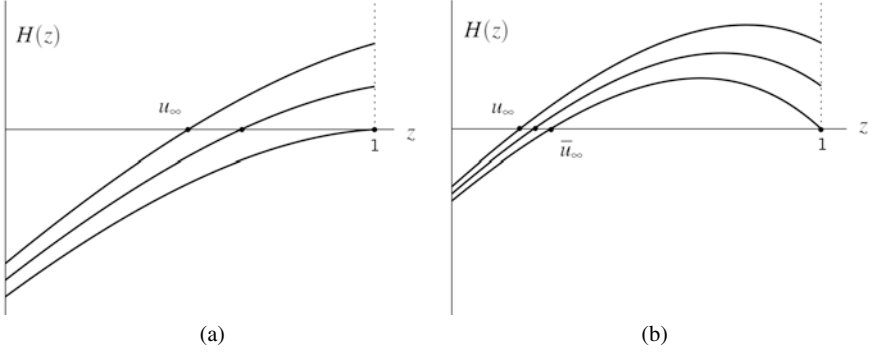


Fig. 8.10 The *pandemic* case. Here $v_0 \ll 1$, $u_0 \approx 1$ and $w_0 = 0$, then $H(1) = 1 - u_0 \approx 0$ and the solution is different corresponding to the two cases $R_0 < 1$ and $R_0 > 1$ respectively shown in panel (a) and (b). In the limit as $u_0 \rightarrow 1$ the eventual susceptible fraction u_∞ tends to 1 in case (a), while, in case (b), u_∞ tends to \bar{u}_∞ which is the smallest solution of Equation (8.24)

This effect becomes sharp in the case of a *pandemic*, i.e. when a new infection is introduced into a population that has no immune fraction. In this case we have

$$w_0 = 0, \quad u_0 \approx 1, \quad v_0 \ll 1$$

and the function $H(z)$ becomes

$$H(z) := z - u_0 e^{-R_0(1-z)}. \quad (8.23)$$

As it is clear from the pictures in Fig. 8.10, where the two case are plotted, we see that in the limit as $u_0 \rightarrow 1$, i.e. as $v_0 \rightarrow 0$, the final size u_∞ is determined by the limiting equation

$$z - e^{-R_0(1-z)} = 0. \quad (8.24)$$

Namely, if $R_0 \leq 1$ then $u_\infty = 1$ and, if $R_0 \geq 1$, u_∞ is identified as the smallest solution to the limiting equation. This can be stated as a second form of the *threshold theorem* in the case of a *pandemic*:

- if $R_0 \leq 1$, as the initial fraction of infected individuals tends to 0, the fraction that gets infected goes to 0;
- if $R_0 > 1$, as the initial fraction of infected individuals goes to 0, the fraction that gets infected tends to the positive value $\bar{w}_\infty = 1 - \bar{u}_\infty$.

The fraction $\bar{w}_\infty = 1 - \bar{u}_\infty$ can be considered a measure of the impact of an epidemic. It represents the fraction of the population that gets eventually removed when an epidemic starts in a totally susceptible population where an infinitesimally small fraction of infected individuals is introduced. The quantity w_∞ is a function of R_0

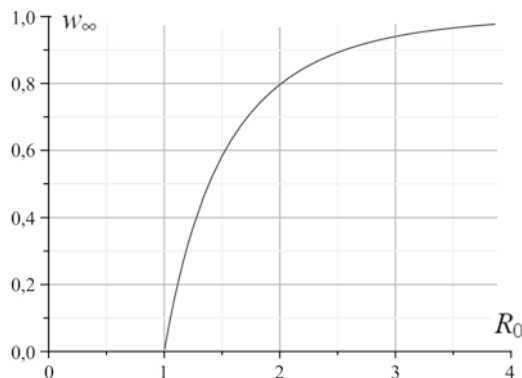


Fig. 8.11 The infected fraction w_0 as a function of R_0 . For $R_0 = 2$ more than 80% of the population gets infected, while for $R_0 = 4$ this fraction goes beyond 98

only, which is plotted in Fig. 8.11; one sees, for instance, that for $R_0 = 2$ more than 80% of the population gets infected, while for $R_0 = 4$ this fraction goes beyond 98%.

We have seen that the parameter R_0 defines the final impact of a pandemic and, together with knowledge of the initial immune fraction w_0 , of any epidemic, as u_∞ is a root of (8.22). The threshold theorem (8.17) shows how R_0 and the actual fraction of susceptibles can determine if an epidemic outbreak can occur; more quantitatively, linearizing (8.9) near an initial condition (u_0, v_0) with $v_0 \approx 0$, the second of (8.9) becomes

$$v'(\tilde{t}) \approx (R_0 u_0 - 1)v(\tilde{t})$$

that shows that the infected fraction initially grows exponentially. Going back to the original (dimensional) time units t , one can say that the initial rate of increase of infectives (either in numbers or in fraction) is

$$r = \gamma(R_0 u_0 - 1). \quad (8.25)$$

It can then be seen that many epidemic features depend on the value of R_0 . In Sect. 8.5 we will discuss how knowledge of R_0 can be used to guide sanitary control measures and prevention.

The interpretation by Kermack-McKendrick and mass-action law

The SIR model (8.7) considered in this section is commonly named after Kermack and McKendrick who in a celebrated series of papers ([10]- [12]) set forward the basic elements of epidemic description. Their model was based on a framework including the time elapsed since infection as a variable, that we will present in Sect. 8.6, while in this section we discuss the ODE version.

Indeed, our model (8.7), though mathematically equivalent to the original Kermack-McKendrick model, differs in the interpretation. In fact, Kermack and McKendrick allow for disease-induced deaths, and, as already remarked, the class of removed individuals includes not only recovered and immune (like us) but also individuals that have died of the disease and those that have been quarantined. Hence, the total active population $N(t)$ cannot be constant, and assumption (8.2) would lead into a different model. However, Kermack and McKendrick assume that the contact rate has the form

$$c(N) = c_0 N \quad (8.26)$$

so that the incidence $j(t)$ has the constitutive form

$$j(t) = \lambda(t)S(t) = c_0 \chi I(t)S(t) := \beta I(t)S(t) \quad (8.27)$$

and the model reads

$$\begin{cases} S'(t) = -\beta I(t)S(t) \\ I'(t) = \beta I(t)S(t) - \gamma I(t) \\ R'(t) = \gamma I(t). \end{cases}$$

System (8.7) is the same as this one, but for a different constant (here β/N is replaced by β). The basic reproduction number for this system is then

$$R_0 = \frac{c_0 \chi N(0)}{\gamma}$$

while the threshold condition reads

$$\frac{c_0 \chi S(0)}{\gamma} > 1.$$

Some authors call (8.27) as the ‘standard mass action law’ for new infections, while (8.3) is named the ‘true mass-action law’.

8.3 Stochastic modeling of an epidemic outbreak

Here we consider a stochastic version of the SIR epidemic model in a closed population. We follow the same philosophy used in Chap. 4; thus we assume that the size of susceptible and infected populations can consist only of integer numbers, and we consider a Markov process on the resulting discrete space, in which the infinitesimal transition rates correspond to the fluxes of the differential equations.

If the total population size is N , the possible values for the pair $(S(t), I(t))$ representing the number of susceptible and infected individuals at time t are

$$E = \{(k, j) \in \mathbb{N}^2 : k + j \leq N\}.$$

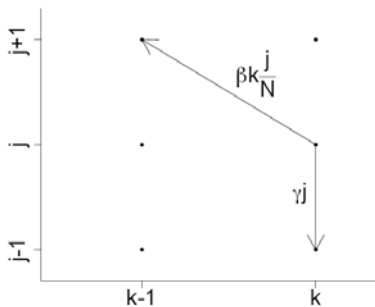


Fig. 8.12 An illustration of the infinitesimal transitions for the stochastic SIR model

As we consider a closed population, without births or deaths, the only possible infinitesimal transitions correspond to a new infection, or to a recovery of an infected individual. We write the transitions as:

- $(k, j) \rightarrow (k-1, j+1)$ at rate $\beta j \frac{k}{N}$ (infection);
 - $(k, j) \rightarrow (k, j-1)$ at rate γj (recovery).
- (8.28)

The rates correspond exactly to the classical *SIR* deterministic model, noting that the state (k, j) means $S(t) = k, I(t) = j$ (see Fig. 8.12 for a graphical illustration).

A possible way to analyze the process is by finding the probabilities that the pair $(S(t), I(t))$ is in any given state. Let us then fix the initial state at time 0 at (m, a) ($S(0) = m, I(0) = a$), with $m + a \leq N$ ($m + a = N$ in case of a pandemic) and generally a rather small (the interest is in the outcome of the introduction of a few infected individuals).

Letting then

$$P_{(k,j)}(t) = \mathbb{P}(S(t) = k, I(t) = j)$$

the same derivation leading to Kolmogorov forward equations (D.2) now ensures that

$$P'_{(k,j)}(t) = \beta(k+1) \frac{j-1}{N} P_{(k+1,j-1)}(t) + \gamma(j+1) P_{(k,j+1)}(t) - \left(\beta k \frac{j}{N} + \gamma j \right) P_{(k,j)}(t). \quad (8.29)$$

Equation (8.29) is a system of (linear) differential equations that has to be completed by the appropriate initial conditions. As it was assumed $u(0) = m, v(0) = a$, then

$$P_{(m,a)}(0) = 1, \quad P_{(k,j)}(0) = 0 \quad \text{for } (k, j) \neq (m, a).$$

As (8.29) is a linear system, it is well known that it has a unique solution: this in principle yields all information about the process. Indeed, several methods have been employed, especially using the generating function, to obtain explicit expressions for the solution. However the expressions obtained in this way are rather cumbersome, and do not easily yield picturesque results.

We concentrate here only on one aspect of the problem, that of the final size of the epidemic, i.e. the number of individuals that get infected. As we are modeling a Markov process on a finite state space in which all the states $(k, 0)$ are absorbing (see (8.28)), the general theory implies that:

with probability 1, there exist $T > 0$ and $k \leq m$ such that

$$(S(t), I(t)) \equiv (k, 0) \quad \text{for } t > T.$$

The aim is then to understand what the distribution of such final values k is. Precisely, we define

$$W = m - \lim_{t \rightarrow \infty} S(t) \quad (\text{total number of infected individuals})$$

and we wish to obtain

$$\mathbb{P}(W = w) \quad \text{for all } 0 \leq w \leq N.$$

To this purpose, since we are not interested in time, we can reduce the study to that of the jump Markov chain, because this shares the asymptotic behavior with the continuous-time Markov process.

Let us then consider the Markov chain (X_n, Y_n) , starting with $X_0 = m, Y_0 = a$, and defined by the transition probabilities

$$\begin{aligned} \mathbb{P}(X_{n+1} = k-1, Y_{n+1} = j+1 | X_n = k, Y_n = j) &= \frac{\beta k \frac{j}{N}}{\beta k \frac{j}{N} + \gamma j} = \frac{R_0 \frac{k}{N}}{R_0 \frac{k}{N} + 1} \quad k, j > 0 \\ \mathbb{P}(X_{n+1} = k, Y_{n+1} = j-1 | X_n = k, Y_n = j) &= \frac{\gamma j}{\beta k \frac{j}{N} + \gamma j} = \frac{1}{R_0 \frac{k}{N} + 1} \quad k \geq 0, j > 0 \\ \mathbb{P}(X_{n+1} = k, Y_{n+1} = 0 | X_n = k, Y_n = 0) &= 1 \quad k \geq 0 \end{aligned}$$

where $R_0 = \beta/\gamma$ (as in the deterministic model).

We can now consider $W = m - \lim_{n \rightarrow \infty} X_n$. The left panel of Fig. 8.13 shows a trajectory of the process leading to $W = 15$. In order to compute $\mathbb{P}(W = 15)$, we would need to sum the probabilities of all such trajectories.

For small numbers, this can be easily accomplished: for instance, the right panel of Fig. 8.13 shows that, if $a = 1$, there are only two trajectories leading to $W = 2$.

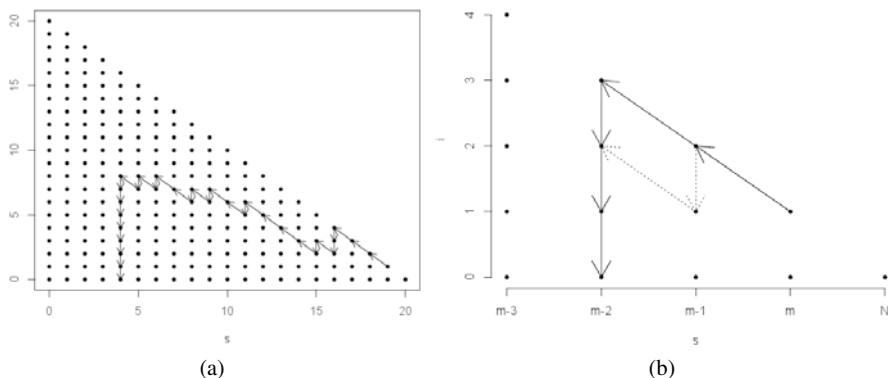


Fig. 8.13 (a) the state space and one trajectory for $N = 20$, $m = 19$, $a = 1$; (b) the two trajectories of the chain (X_n, Y_n) with $a = 1$ leading to $W = 2$

Then

$$\begin{aligned} \mathbb{P}(W = 2) = & \frac{R_0 \frac{m}{N}}{R_0 \frac{m}{N} + 1} \frac{R_0 \frac{m-1}{N}}{R_0 \frac{m-1}{N} + 1} \frac{1}{(R_0 \frac{m-2}{N} + 1)^3} \\ & + \frac{R_0 \frac{m}{N}}{R_0 \frac{m}{N} + 1} \frac{1}{R_0 \frac{m-1}{N} + 1} \frac{R_0 \frac{m-1}{N}}{R_0 \frac{m-1}{N} + 1} \frac{1}{(R_0 \frac{m-2}{N} + 1)^2}. \end{aligned} \quad (8.30)$$

Clever combinatorial computations lead to an asymptotic formula for $\mathbb{P}(W = w)$ for any $w \in \mathbb{N}$. Precisely, one obtains

$$\lim_{\substack{N \rightarrow \infty \\ m/N \rightarrow u_0}} \mathbb{P}(W = w) = \frac{a}{a+2w} \binom{a+2w}{w} \left(\frac{R_0 u_0}{R_0 u_0 + 1} \right)^w \left(\frac{1}{R_0 u_0 + 1} \right)^{a+w}. \quad (8.31)$$

The steps leading to (8.31) (see [1] for details) are, on the one hand, realizing that any such trajectory will contain exactly w infections and $a + w$ recoveries (those of new infected plus those of initial ones), on the other hand, that any fraction $(m - k)/N$ with $k \leq w$ will converge (like m/N) to u_0 as $N \rightarrow \infty$. Thus the probability of all trajectories leading to $W = w$ will converge to the same value, as $N \rightarrow \infty$; compare, for instance, the two terms in (8.30). Finally, one needs to count the number of such trajectories and this can be shown to be $\frac{a}{a+2w} \binom{a+2w}{w}$, leading to (8.31).

Defining now $g_a(w)$ as the right hand side of (8.31):

$$g_a(w) = \frac{a}{a+2w} \binom{a+2w}{w} \left(\frac{R_0 u_0}{R_0 u_0 + 1} \right)^w \left(\frac{1}{R_0 u_0 + 1} \right)^{a+w}, \quad (8.32)$$

it is not difficult to show that in almost all cases $g_a(w+1) < g_a(w)$; precisely for all $w \geq 0$, if $a \leq 4$ and for w large enough if $a > 4$. Furthermore

$$\lim_{w \rightarrow \infty} \frac{g_a(w+1)}{g_a(w)} = \frac{4R_0u_0}{(1+R_0u_0)^2} \leq 1$$

with strict inequality, unless $R_0u_0 = 1$.

This shows that asymptotically $\mathbb{P}(W = w)$ decreases with w with a decay of exponential type (unless $R_0u_0 = 1$). There is however another important property. Thanks to the identity

$$\sum_{k=0}^{\infty} \frac{a}{a+2k} \binom{a+2k}{k} p^k q^k = p^{-a}, \quad (8.33)$$

where $q = 1 - p$ and $\frac{1}{2} \leq p \leq 1$, one obtains

$$\sum_{w=0}^{\infty} g_a(w) = \left(\min \left\{ 1, \frac{1}{R_0u_0} \right\} \right)^a. \quad (8.34)$$

Note that, if $R_0u_0 \leq 1$, then $g_a(w)$ is a proper distribution because

$$\sum_{w=0}^{\infty} g_a(w) = 1,$$

so that $g_a(w)$ yields a complete approximation to $\mathbb{P}(W = w)$ for N large.

Instead, if $R_0u_0 > 1$ we have

$$\sum_{w=0}^{\infty} g_a(w) = (R_0u_0)^{-a} < 1$$

and something is missing. Obviously we have

$$\lim_{N \rightarrow \infty} \left(\sum_{w=0}^{\infty} \mathbb{P}(W = w) \right) = \lim_{N \rightarrow \infty} 1 = 1$$

while we obtained

$$\sum_{w=0}^{\infty} \left(\lim_{N \rightarrow \infty} \mathbb{P}(W = w) \right) = \sum_{w=0}^{\infty} g_a(w) < 1.$$

This means that there exists some function $\phi(N)$ such that $\lim_{N \rightarrow \infty} \phi(N) = +\infty$ and

$$\lim_{N \rightarrow \infty} \left(\sum_{w \geq \phi(N)} \mathbb{P}(W = w) \right) = 1 - \sum_{w=0}^{\infty} g_a(w) = 1 - \frac{1}{(R_0u_0)^a}.$$

We have then obtained a form of the stochastic threshold theorem:

- if $R_0 u_0 \leq 1$, the probability of having an epidemic of size w is well approximated (when N is large) by the probability distribution $g_a(w)$, which is close to exponential; and there is probability 0 of having an epidemic of size comparable to population size (a ‘major epidemic’);
- if $R_0 u_0 > 1$, there is probability $1 - \frac{1}{(R_0 u_0)^a}$ of having an epidemic of large size (comparable to N).
With probability $\frac{1}{(R_0 u_0)^a}$ there will instead be a small epidemic; the probability of a final size w would again be approximated by $g_a(w)$, which in this case is a defective probability distribution.

These results concern the limit as the population size N goes to ∞ . To understand what can happen in real populations of finite size, one may look at the outcome of simulations with finite population size. Figure 8.14 shows the final epidemic size for $N = 100$ and $N = 1000$ for three different values of R_0 . In the simulations with $R_0 = 2$, the division into small and large epidemics can be clearly seen already for $N = 100$ and becomes very sharp for $N = 1,000$. It can also be seen that the distribution of small epidemics fits very well with the (defective) distribution $g_a(w)$, and that the large epidemics yield a final size that is distributed almost symmetrically around the value predicted by the deterministic model.

When $R_0 = 1.25$ and $N = 100$, while a large proportion of epidemics yield a very small epidemic size that is described very well by $g_a(w)$, there are also epidemics of any size up to twice as much what predicted by the deterministic model. For $N = 1,000$ the division into small and large epidemics becomes more apparent, with just a few intermediate epidemics; the large epidemics are also distributed around the deterministic final size.

Finally, when $R_0 = 0.8$, there are only small epidemics, as predicted, and their size follows quite well the distribution $g_a(w)$.

The reader may have noted that the results obtained are very reminiscent of what was obtained for linear birth-and-death processes (stochastic Malthus model). Indeed another approach to obtain the threshold theorem is to approximate the fraction k/N that appears in (8.28) with $u_0 = m/N$.

Indeed, in the limit as $N \rightarrow \infty$, the decrease in the susceptible population will be negligible relatively to N at least in the first phase of the epidemic. Hence, in the first phase of the epidemic, the infected population $v(t)$ will approximately follow a linear birth-and-death process with ‘birth’ rate $\beta u_0 j$ and ‘death’ rate γj .

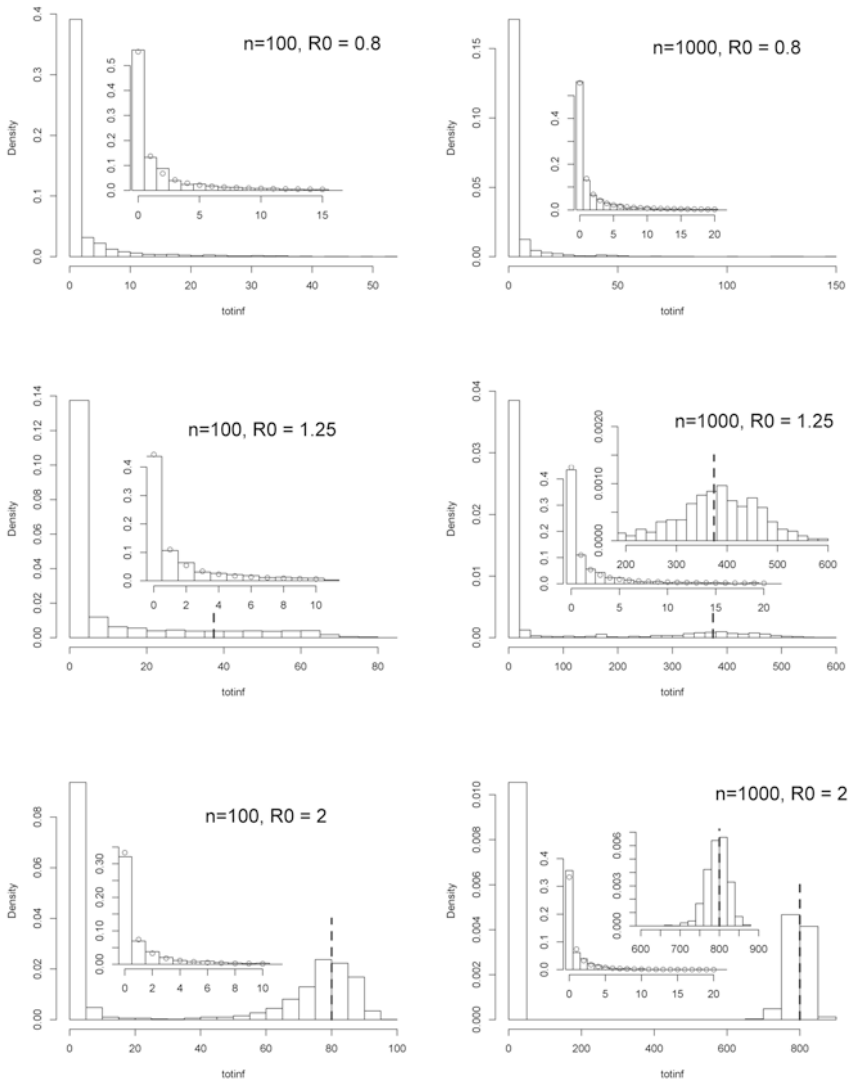


Fig. 8.14 Distribution of final size in simulation of the SIR stochastic model; the panels correspond to different values of population size N and R_0 . All simulations started with $a = 1$ and $m = N - 1$. The insets show enlargements of some parts of the histograms; the circles show the value of $g_a(w)$, while the dashed lines indicate the final size according to the deterministic model

From the results on birth-and-death process, we can then conclude that:

the extinction of the infected population (i.e. the early end of the epidemic) occurs

- with probability 1 if $\beta u_0 \leq \gamma$ (i.e. $R_0 u_0 \leq 1$) ;
- with probability $\left(\frac{\gamma}{\beta u_0}\right)^a$ if $\beta u_0 > \gamma$ (i.e. $R_0 u_0 > 1$).

Note that in the latter case we have exactly the probability of a minor epidemic found above. Furthermore, $g_a(w)$ is the distribution of the number of births in a birth-and-death process. Precisely, if $\lambda_i = \lambda i$, $\mu_i = \mu i$ and the initial population size is a , the probability that exactly w births occur is

$$\frac{a}{a+w} \binom{a+2w}{w} \left(\frac{\lambda}{\lambda+\mu}\right)^w \left(\frac{\mu}{\lambda}\right)^{a+w}.$$

This is $g_a(w)$ setting $R_0 u_0 = \lambda/\mu$.

If the infected population does not get extinct in the initial phase, then it increases to a size comparable to population size N and the linear approximation can no longer be justified. At that point, however, the trajectory can be approximated by the deterministic model, as the fractions of both susceptible and infected individuals are large enough. In the final phase of the epidemic, there will be only a few infected individuals, so that a stochastic model would be required again.

This intuitive description can be justified rigorously but requires methods much more advanced than what used here (see [3]). We are content with showing some simulations of the SIR model, compared with the deterministic system. It can be seen (Fig. 8.15) that the main difference is in the time required for the epidemic to take

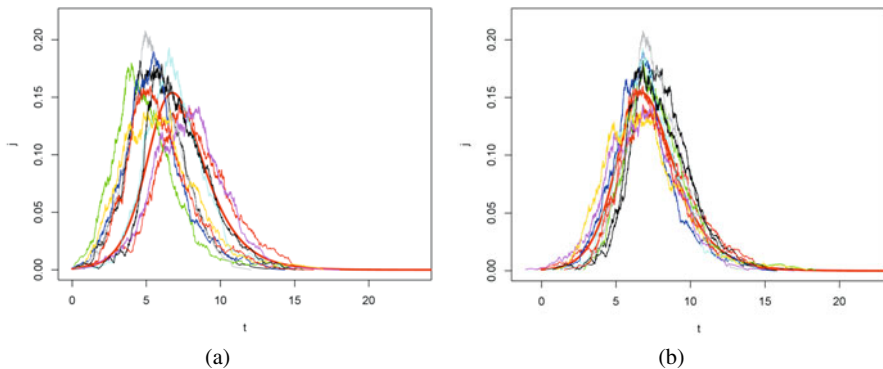


Fig. 8.15 (a) Infected fraction vs. time for some simulations of the SIR stochastic model that do not undergo early extinction; parameter values are $\sigma = 2$, $\gamma = 1$, $N = 1,000$ with initial values $m = 999$, $a = 1$. the thicker line is the deterministic solution with the same parameters and initial values; (b) The same curves after having adjusted the epidemic peak of any simulation to the peak of the deterministic solution

off. If all the different simulations are aligned at the epidemic peak, then they look rather similar (already with $N = 1,000$) to the deterministic model, though stochastic effects can be clearly seen.

8.4 Disease endemicity

The analysis of the simple outbreak of an epidemics shows that the epidemics stops and decays due to the depletion of susceptibles below the threshold value (8.18). Thus sustained infections require the replacement of susceptibles.

Two different mechanism may lead to such replacement and consequently to *endemic states* of the disease. The first is related to non-immunizing diseases, the other to demographic input of susceptible newborns.

To examine the first case we consider the S-I-S type model of Fig. 8.4, with the force of infection in the form (8.6). Then we have the system of equations (compare with (8.4))

$$\begin{cases} S'(t) = -\frac{\beta}{N}I(t)S(t) + \gamma I(t), \\ I'(t) = \frac{\beta}{N}I(t)S(t) - \gamma I(t). \end{cases} \quad (8.35)$$

Here the class of removed individuals is absent and, since we have

$$S(t) + I(t) = S(0) + I(0) = N,$$

the system can be reduced to a single equation on the state variable $I(t)$.

Adopting the dimensionless variables (8.8) used in the previous case, we have the following equation for the infective fraction $v(t)$

$$v'(t) = R_0 (v^* - v(t)) v(t),$$

where R_0 is basic reproduction number defined in (8.6) and

$$v^* = 1 - \frac{1}{R_0}$$

is the endemic state that exists only for $R_0 > 1$ and increases with R_0 . This equation can be explicitly solved, but even without solving it, an analysis of the intervals where $v'(t) > 0$ or < 0 leads to the following dichotomy:

- if $R_0 \leq 1$ then $v'(t) < 0$ and $\lim_{t \rightarrow \infty} v(t) = 0$;
- if $R_0 > 1$ then $\lim_{t \rightarrow \infty} v(t) = v^*$.

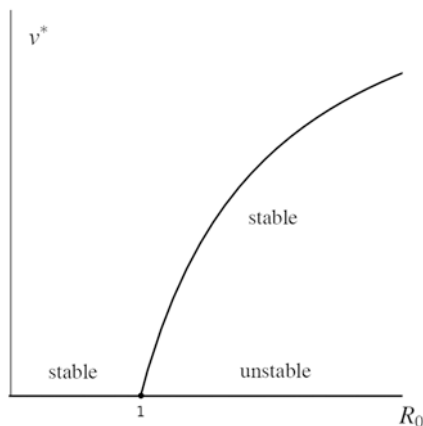


Fig. 8.16 Bifurcation diagram for problem (8.35). At $R_0 = 1$ the endemic state arises from the disease-free one and inherits its stability

Thus we see that R_0 acts again to determine a threshold for two alternatives. Here, extinction of the disease is opposed to the existence of a globally attractive endemic state v^* the size of which is determined by the size of R_0 . This scenario is described in Fig. 8.16 where bifurcation of steady states and exchange of stability is shown.

In order to analyze the effect of demographic dynamics on disease endemicity, we consider the previous S-I-R model including a simple *neutral* Malthusian dynamics (see Sect. 8.7 for other assumptions). Precisely, we make the two following assumptions:

- births and deaths occur at the same rate so that total population size does not change with time;
- all newborns are susceptibles.

Thus, denoting by μ both fertility and mortality we obtain the model

$$\begin{cases} S'(t) = \mu N - \frac{\beta}{N} I(t) S(t) - \mu S(t) \\ I'(t) = \frac{\beta}{N} I(t) S(t) - (\gamma + \mu) I(t) \\ R'(t) = \gamma I(t) - \mu R(t), \end{cases} \quad (8.36)$$

where the other parameters are as in (8.4).

As the first two equations are independent of the third, while, if needed, $R(t)$ can be easily obtained as $R(t) = N - S(t) - I(t)$, we drop the third equation, and consider

the reduced system

$$\begin{cases} S'(t) = \mu N - \frac{\beta}{N} I(t) S(t) - \mu S(t) \\ I'(t) = \frac{\beta}{N} I(t) S(t) - (\gamma + \mu) I(t) \end{cases} \quad (8.37)$$

completed with initial conditions $S(0) = S_0 \geq 0$, $I(0) = I_0 \geq 0$.

In this model, the average duration of the infection is affected also by the possibility of dying for natural reasons; as the total exit rate from the infective class is $\gamma + \mu$, the average length of the infectious period is $\tau = \frac{1}{\gamma + \mu}$. Hence, the expression (8.10) of the basic reproduction number R_0 must be changed into

$$R_0 = \frac{c\chi}{\gamma + \mu}, \quad (8.38)$$

representing the number of new infective individuals produced by an infected, during all the infectious period.

The average time τ is also a natural unit to adopt to scale the system. Performing the transformation

$$t \rightarrow \tilde{t} = (\gamma + \mu)t, \quad S \rightarrow u = \frac{S}{N}, \quad I \rightarrow v = \frac{I}{N}, \quad R \rightarrow w = \frac{R}{N},$$

we get the dimensionless equations

$$\begin{cases} u'(\tilde{t}) = \alpha(1 - u(\tilde{t})) - R_0 u(\tilde{t}) v(\tilde{t}), \\ v'(\tilde{t}) = (R_0 u(\tilde{t}) - 1)v(\tilde{t}), \end{cases} \quad (8.39)$$

where the dimensionless parameter

$$\alpha = \frac{\mu}{\gamma + \mu} \quad (8.40)$$

is the demographic mortality measured in the new time units τ .

Existence and properties of equilibria again depend on the value of the basic reproduction number R_0 . In fact, setting equal to 0 the right hand side of (8.39), we find the following equilibria:

- disease free equilibrium F :

$$u^* = 1, \quad v^* = 0;$$

- endemic equilibrium E :

$$u^* = \frac{1}{R_0}, \quad v^* = \alpha \left(1 - \frac{1}{R_0} \right).$$

While the disease free equilibrium F always exists, the endemic one E belongs to the feasible region $\{u \geq 0, v \geq 0, u + v \leq 1\}$ only for $R_0 > 1$.

Equilibrium stability is also driven by R_0 as can be seen by linearization of (8.37) at these equilibria. The Jacobian matrix at $F \equiv (1, 0)$ is

$$J(F) = \begin{pmatrix} -\alpha & -R_0 \\ 0 & R_0 - 1 \end{pmatrix},$$

with the eigenvalues $\lambda_1 = -\alpha$ and $\lambda_2 = R_0 - 1$; this shows that F is stable for $R_0 < 1$ and unstable for $R_0 > 1$.

As for the endemic equilibrium E (existing only when $R_0 > 1$), the Jacobian is

$$J(E) = \begin{pmatrix} -\alpha R_0 & -1 \\ \alpha(R_0 - 1) & 0 \end{pmatrix}.$$

Since

$$\text{trace } J(E) = -\alpha R_0 < 0, \quad \det J(E) = \alpha(R_0 - 1) > 0$$

the eigenvalues have negative real parts and E is asymptotically stable. In conclusion we have:

the disease-free equilibrium F is asymptotically stable as $R_0 < 1$ and unstable as $R_0 > 1$, when the endemic equilibrium E exists and is asymptotically stable.

This statement is illustrated in the bifurcation graph of Fig. 8.17, where it is also indicated that the endemic state E is a stable node for R_0 sufficiently close to 1 or

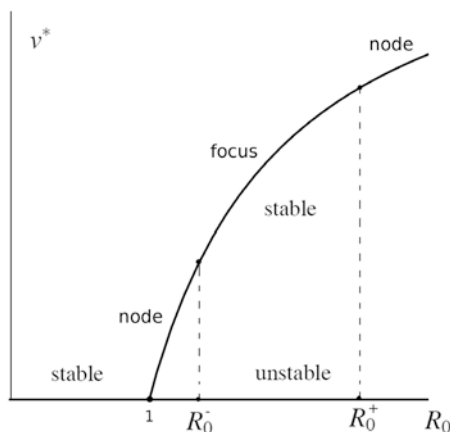


Fig. 8.17 Bifurcation diagram for problem (8.37). An endemic state arises at $R_0 = 1$ and is always asymptotically stable; its eigenvalues are complex for $R_0 \in (R_0^-, R_0^+)$

sufficiently large, but there exist a bounded interval (R_0^-, R_0^+) for $R_0 \in$ such that E is a stable focus and the convergence to equilibrium is oscillatory.

Computing explicitly the eigenvalues of $J(E)$, one finds that

$$R_0^\pm = \frac{2}{\alpha} \left(1 \pm \sqrt{1 - \alpha} \right) > 1$$

and, for $R_0 \in (R_0^-, R_0^+)$,

$$\lambda_\pm = \frac{1}{2} \left(-\alpha R_0 \pm i \sqrt{4\alpha R_0 - \alpha^2 R_0^2 - 4\alpha} \right).$$

From the eigenvalues $\lambda_\pm = a \pm i\omega$, one can obtain an approximation of the time \tilde{T} elapsed from one peak to another, and the approximate damping Δ of the solution after one oscillation. In the scaled time units $\tilde{T} = \frac{2\pi}{\omega}$, and moving to the original time units:

$$T = \frac{2\pi\tau}{\omega} = \frac{4\pi}{(\mu + \gamma) \sqrt{4\alpha R_0 - \alpha^2 R_0^2 - 4\alpha}}, \quad \Delta = e^{a\tilde{T}} = e^{-\alpha R_0 \tilde{T}/2}. \quad (8.41)$$

Note that for most common human diseases, the average infectious period is much shorter than the average life-time, i.e. α is very small, of the order $10^{-2} - 10^{-4}$. Hence $R_0^- \approx 1 + \frac{\alpha}{4}$ is very close to 1, and $R_0^+ \approx \frac{4}{\alpha}$ is very large, so that necessarily convergence to equilibrium will be oscillatory.

Finally, it is possible to show that the stability is actually global. In fact, the general theory of planar systems guarantees that the previous stability properties of the steady states are global if we can exclude existence of periodic solutions for the system. Indeed we can show that (8.39) has no periodic solutions, via the Bendixson-Dulac principle. In fact, using

$$D(u, v) = \frac{1}{uv}$$

as an auxiliary function, we have

$$\text{Div} \left(\frac{\alpha}{uv} - R_0 - \frac{\alpha}{v}, R_0 - \frac{1}{u} \right) = -\frac{\alpha}{u^2 v} < 0,$$

thus excluding the possibility of periodic solutions in the positive quadrant. Possible trajectories in the phase plane (u, v) are shown in Fig. 8.18.

One can obtain the same result, through La Salle Theorem, using the Lyapunov function (see Problem 8.1)

$$V(u, v) = u - u^* \log(u) + v - v^* \log(v). \quad (8.42)$$

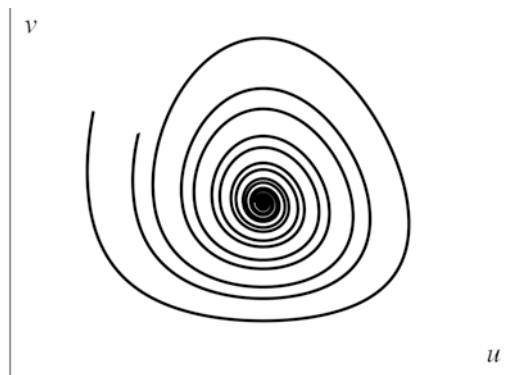


Fig. 8.18 Sample solutions of system (8.39). Here $R_0 = 10$, $\alpha = 2.5 \times 10^{-4}$, hence $R_0 \in (R_0^-, R_0^+)$. These values correspond to realistic values for measles with $\gamma = 52$ (years $^{-1}$) and $\mu = 1.3 \times 10^{-2}$ (years $^{-1}$), giving a peak to peak period $T \approx 2$ (years) (see (8.41)), in agreement with the observed periodicity of the disease

This is especially interesting, because this approach can be extended to higher-dimensional systems, such as an SEIR model.

Recurrent outbreaks of epidemics

The data presented in Figs. 8.1, 8.2 and 8.3 show recurrent outbreaks of epidemics according to a somewhat regular pattern that suggest periodicity. In all cases one sees annual peaks in the number of observed cases, but Fig. 8.2 (measles) shows also a biennial cycle of much larger amplitude; in other datasets, measles shows instead triennial cycles, or a mixture of biennial and triennial, or sometimes just annual cycles.

These cycles pose the problem of identifying the mechanisms that produce the pattern, both qualitatively and quantitatively. While annual cycles may simply depend on regular changes in contact rates (due, for instance, to climate or school-year), longer cycles have long puzzled investigators.

Indeed, model (8.37) was developed also with the aim of explaining cycles as arising from the interaction of the disease with the demography of the population: after one epidemic event, the susceptible fraction of the population becomes too low to support the epidemic process, and replenishment of susceptibles through new births is needed to support a new epidemic outbreak. As shown in Sect. 8.4, the model is actually able to produce oscillations, but only damped.

An interesting observation is that their period, as estimated from (8.41), roughly matches with the observations. In fact, referring to the values in [1], Table 4.1, we see that measles is characterized by R_0 of the order of 10 and an infectious period one week which gives $\gamma \approx 50$ (years $^{-1}$). Moreover, we can

estimate mortality rate $\mu \approx 1 - 1.5 \times 10^{-2}$ (years $^{-1}$) corresponding to an average life of 65–100 years, obtaining the parameter values to be used in formula (8.41):

$$R_0 \approx 10, \quad \alpha \approx 2 - 3 \times 10^{-4}$$

yielding $T \approx 2.4 - 3$ years, in good agreement with the observed data.

The problem remains that model (8.37) does not account for sustained oscillations. A possible explanation for cycle sustained oscillation comes from the analysis of SIR models with periodic contact rates. It has been shown that, in a range of parameter values, the exogenous annual periodicity interacts with the intrinsic periodicity of the system to produce cycle oscillations of a period close to those of damping oscillations. For other parameter values, such a model can also produce chaotic solutions (see for instance [9]).

Other explanations rely on intrinsic stochasticity. Modeling the fluctuations around the deterministic equilibrium through a linear stochastic differential equation, one obtains solutions that (though stochastic) resemble periodic cycles.

8.5 R_0 : herd immunity, vaccination, estimation

We have previously seen that in the long-term perspective, the endemicity of an infection is related to the basic reproduction number R_0 . This parameter in fact can be viewed as determining the success of the infection in invading the disease-free state. Indeed, if $R_0 > 1$, the establishment of a disease as endemic can be produced by a single infective individual who enters into a disease free population composed by all susceptibles; at the end of the infection period, this infective will be more than “replaced” with R_0 infectives, producing an epidemic outbreak that, after several waves, will drive the population to the globally attractive endemic state.

Of course, if for some reason, part of the population is initially immune and the number of susceptibles is too low, the epidemic outbreak is not going to occur. This situation is called *herd immunity* and by itself is not maintained in the long run, because of the continuous replacement of susceptibles by newborns, and perhaps of also by the decay of immunity.

Vaccination, when available, is an effective intervention to keep a population protected by an infection, but it must be administered at a sufficiently high rate in order to guarantee herd immunity, namely to lower the effective reproduction number below 1. In other words, knowing R_0 , we can estimate how large must the vaccinated fraction be.

In fact, assuming that all individuals are initially susceptible and that a vaccine is available, if a fraction

$$w_0 \geq 1 - \frac{1}{R_0}$$

is effectively vaccinated (i.e., the vaccine has worked and the individual is now immune) before the introduction of the infecting agent, then the susceptible fraction becomes

$$u_0 = (1 - w_0) \leq \frac{1}{R_0},$$

so that $R_0 u_0 \leq 1$ and a major epidemic is avoided.

Similar reasonings can be applied in the case of interventions (such as school closures, prohibitions of large meetings...) that reduce the contact rate. Assuming it were possible to reduce on average the contacts by a factor ρ to reach a new value $\tilde{c} = \rho c$, the basic reproduction number would change into

$$\tilde{R}_0 = \rho R_0.$$

An epidemic will then be avoided if and only if $\tilde{R}_0 \leq 1$, i.e.

$$\rho \leq \frac{1}{R_0}.$$

The same ideas can be used in a long term perspective for endemic infections. Vaccination strategies generally rely on vaccinating newborns or very young children. We can modify model (8.39), assuming that a certain fraction p is effectively vaccinated at birth.

In this case the first equation in (8.39) becomes

$$u'(t) = \alpha(1 - p - u(t)) - R_0 u(t)v(t).$$

The infected fraction at the endemic equilibrium becomes

$$v^* = \alpha \left(1 - p - \frac{1}{R_0} \right)$$

if $p < 1 - \frac{1}{R_0}$, while the infection-free state becomes asymptotically stable if $p \geq 1 - \frac{1}{R_0}$. The above threshold value, sometimes denoted as

$$p_c = 1 - \frac{1}{R_0},$$

is named the *critical vaccination ratio*, meaning that it is the effective vaccination fraction that has to be achieved for eradication of the infectious disease.

Similar results can be obtained (Problem 8.5), if one assumes that vaccinations, instead of being directed to newborns, are distributed at random to all individuals.

Given the central role played by the basic reproduction number R_0 , it is important to be able to estimate this parameter from observed data and to measure the effectiveness of interventions through the estimated reduction of its value. It is very unlikely, for human infections, that one can measure R_0 directly, as it depends on contact rates and probability of infecting contacts. Thus, though *a priori* information

may exist about γ and χ , a *posteriori* analysis of epidemiological data is essential to provide estimate of R_0 .

Here we present some simple methods for estimating R_0 , without delving into the statistical arena of estimating parameters for nonlinear models.

A first tool for this purpose is formula (8.21) that involves the susceptible fraction before and after a single epidemic outbreak. In fact, from (8.21), approximating $v_0 \approx 0$ so that $u_0 \approx 1 - w_0$, we get

$$R_0 = \frac{\ln(u_\infty) - \ln(u_0)}{u_\infty - u_0}.$$

Of course the estimation of both u_∞ and u_0 have to be performed through analysis of data such as serological surveys and/or sample inquiries. In case of a pandemic outbreak we can take $u_0 = 1$.

Another method to estimate R_0 is based on the assumption that an infection is at the equilibrium endemic state. In fact, we have

$$R_0 = \frac{1}{u^*},$$

and, again, u^* can be measured by serological surveys.

The previous method suffers from the need of obtaining serological surveys (which is not always easy), and from the fact that the immune fraction depends heavily on age, so that it is not easy defining the average susceptible fraction. It is instead possible relating R_0 to the average age of attack A , i.e. the *age of the individual when being infected*. In fact, A is the average time spent as a susceptible before becoming an infective, and (by the same argument used for estimating average infectious period) is equal to the inverse of the force of the infection at the endemic equilibrium, i.e.

$$A = \frac{1}{\alpha(R_0 - 1)}.$$

Here A should be measured in units of τ . Measuring it in any time unit, we then obtain (see (8.40)) the following formula to estimate R_0

$$R_0 = 1 + \frac{L}{A},$$

where L is the average length of life.

All the previous methods of estimation of R_0 require data coming from previous epidemics and give information to face an endemic infection or possible re-emergences of the same infection. On the other hand, in front of a new infection, we need to obtain early estimates using data relative to the first phase of an outbreak. To this aim, we may compare data to the initial growth predicted by the model. In fact, recall that model (8.4) predicts that initially the number of infectives should grow exponentially at rate (8.25); the same holds for related quantities, as the incidence $j(t)$. Indeed notifications of new cases (which we can consider incidence) in an epidemic outbreak generally show an initial phase of exponential growth; by an-

alyzing data in logarithmic scale (as discussed in the first chapter) one can estimate the increase rate r .

Using (8.25), that can be rewritten as

$$r = \gamma(R_e(0) - 1), \quad (8.43)$$

one can estimate

$$R_e(0) \approx 1 + \frac{r}{\gamma} \quad (8.44)$$

where r is the estimate from data, while γ is assumed to be known from clinical data.

An advantage of this method, as well as the one based on average age at infection, is that we do not need to have perfect observations. They work as well with under-reporting (only a fraction of cases are reported), as long as the reported fraction does not change with time (or with age).

8.6 Distributed infection period and variable infectiousness

The models we have discussed in the previous sections are all based on the constitutive assumption (8.6) for the force of infection and on the form (8.1) for the probability an individual is still infective after a time t since infection. In particular the parameters c , χ , γ are all considered constant, disregarding features that may be important in the description of epidemic dynamics.

Extensions of the contact mechanisms, relaxing the assumption of a homogeneously mixing population, or analyzing how the mass-action law should be modified when population size is varying, also because of disease-induced deaths, will be considered in the next sections. In this section, we allow for the parameters χ and γ to depend on the time elapsed since an individual became infected. Considering explicitly this time ('infection age') is especially important when modeling diseases with an appreciable incubation period or long-lasting infections where chances of recovery or death, and infectiousness vary with the time spent as an infected. The recent epidemics by HIV/AIDS spurred the analysis of this type of phenomenology and also the specific features of a disease such as Tuberculosis motivate more structured modeling.

We start from the SIR basic model (8.4) that, in view of our modifications, is more conveniently formulated replacing the variable $I(t)$ with the incidence $j(t)$ for a description in terms of an integro-differential system.

With this choice, in fact, the second equation in (8.7) can be written as

$$I'(t) = j(t) - \gamma I(t)$$

so that we have the following integral expression for $I(t)$

$$I(t) = \int_{-\infty}^t \Pi(t-s) j(s) ds \quad (8.45)$$

based on (8.1) and all the past history of the incidence $j(t)$.

Then, since by (8.6) we have

$$j(t) = \lambda(t)S(t) = \frac{c\chi}{N}I(t)S(t)$$

we have the following integro-differential system in the variables $S(t)$ and $j(t)$ (we may disregard the equation for $R(t)$ since this variable does not appear in the other two equations)

$$\begin{cases} i) & S'(t) = -j(t) & S(0) = S_0, \\ ii) & j(t) = S(t) \int_{-\infty}^t \frac{c\chi}{N} \Pi(t-s)j(s)ds & j(t) = \phi(t) \quad t \in (-\infty, 0], \end{cases} \quad (8.46)$$

where we see how the system at time t depends on the past history of the incidence, weighted by the probability $\Pi(t)$ computed at $(t-s)$ which is the time elapsed since infection.

Indeed, in generalizing the model to include the features discussed above, the main ingredient to be modified is the convolution kernel appearing in the integral equation (8.46)-ii. In fact, on the one hand we can modify $\Pi(t)$ allowing distributions of the time of infection different from (8.1), on the other hand we can replace the constant infectiousness χ with a variable infectiousness depending on the time elapsed since infection $(t-s)$.

As for $\Pi(t)$, we may for instance adopt:

- a gamma distributed time of infection

$$\Pi(t) = (1 + \gamma t)e^{-\gamma t};$$

- a fixed duration of infection θ_+

$$\Pi(t) = \begin{cases} 1 & \text{for } t \leq \theta_+, \\ 0 & \text{for } t > \theta_+. \end{cases}$$

Concerning infectiousness we can consider:

- fading infectiousness

$$\chi(t) = \chi e^{-\delta t};$$

- unimodal peaked infectiousness

$$\chi(t) = \chi t^q e^{-\delta t};$$

- bimodal infectiousness

$$\chi(t) = \chi_1 t^q e^{-\delta_1 t} + \chi_2 e^{-\delta_2 t}.$$

where the constants $\chi, \chi_1, \chi_2, \delta, \delta_1, \delta_2, q$ are all positive. Any possible choice for both $\Pi(t)$ and $\chi(t)$ leads to a kernel

$$K(t) = \frac{c}{N} \chi(t) \Pi(t)$$

and to an integro-differential system of the form

$$\begin{cases} S'(t) = -j(t) & S(0) = S_0, \\ j(t) = S(t) \int_{-\infty}^t K(t-s) j(s) ds & j(t) = \phi(t) \quad t \in (-\infty, 0]. \end{cases} \quad (8.47)$$

The second equation is a convolution equation of Volterra type and its well-posedness can be proved in a standard way, yielding $S(t) \geq 0$ and $j(t) \geq 0$. Hence $S(t)$ is non increasing and $S(t) \rightarrow S_\infty \geq 0$.

We can determine the final size of the susceptible fraction $u_\infty = S_\infty/N$ by manipulating the equations of the system. In fact, by substitution of the first equation into the second, we get

$$\frac{S'(t)}{S(t)} = - \int_{-\infty}^t K(t-s) j(s) ds = \int_0^t K(t-s) S'(s) ds - \int_{-\infty}^0 K(t-s) \phi(s) ds,$$

where the second term on the right accounts for the force of infection that at time t is due to the past history of the incidence. Integrating both sides in the infinite interval $(0, +\infty)$, we have (recall $u(t) = S(t)/N$)

$$\begin{aligned} \ln \left(\frac{u_\infty}{u_0} \right) &= \int_0^{+\infty} \int_0^t K(t-s) S'(s) ds dt - \int_0^{+\infty} \int_{-\infty}^0 K(t-s) \phi(s) ds dt \\ &= \int_0^{+\infty} S'(s) \int_s^{+\infty} K(t-s) dt ds - \Lambda_0 = R_0 (u_\infty - u_0) - \Lambda_0 \end{aligned} \quad (8.48)$$

where

$$R_0 = \int_0^{+\infty} K(s) ds = c \int_0^{+\infty} \chi(s) \Pi(s) ds \quad (8.49)$$

is the (new) basic number of the model and

$$\Lambda_0 = \int_0^{+\infty} \int_{-\infty}^0 K(t-s) \phi(s) ds dt$$

is the probability a susceptible is infected by one individual of the original group of infectives.

Note that, in the case of a constant removal rate (see(8.1)) and a constant infectiousness, (8.49) gives

$$R_0 = c\chi \int_0^{+\infty} e^{-\gamma s} ds = \frac{c\chi}{\gamma},$$

i.e. the previous basic number (8.10). Moreover we also have

$$\Lambda_0 = \frac{c\chi}{N} \int_0^{+\infty} \int_{-\infty}^0 e^{-\gamma(t-s)} \phi(s) ds dt = \frac{R_0}{N} \int_{-\infty}^0 e^{\gamma s} \phi(s) ds \quad (8.50)$$

and, using (8.45),

$$\Lambda_0 = R_0 v_0. \quad (8.51)$$

Note that, if only χ is constant then, whichever be $\Pi(t)$, R_0 can be expressed as

$$R_0 = c\chi \int_0^{+\infty} \Pi(t) dt,$$

where $\int_0^{+\infty} \Pi(t) dt$ is the expected length of infectiousness.

From (8.48) we finally obtain the equation for u_∞

$$u_\infty = u_0 e^{-R_0(u_0 - u_\infty)} - \Lambda_0 \quad (8.52)$$

which, in the case of constant χ and γ , gives back eq. (8.21) (we use (8.50) and the constraint $u_0 + v_0 + w_0 = 1$).

More generally, in the case of a pandemic, when we suppose that $w_0 = 0$ and that $\Lambda_0 \ll 1$, eq. (8.52) is approximated by (8.24), with R_0 defined by (8.49).

Within the framework settled by model (8.47), we can also find the growth rate at the beginning of the epidemics. As in the case of Sect. 8.2 we approximate system (8.47) approximating the susceptible fraction $u(t)$ by the initial value u_0 . Then we are left with the equation

$$j(t) = u_0 N \int_{-\infty}^t K(t-s) j(s) ds, \quad (8.53)$$

and the asymptotic behavior is related to the roots of the characteristic equation

$$1 = u_0 N \int_0^{+\infty} e^{-\lambda s} K(s) ds,$$

obtained by looking for exponential solutions $j(t) = e^{\lambda t}$. Actually such equation is quite similar to the characteristic equation (2.30) (and eq. (8.53) is quite similar to (2.24)) so that we know that it has a unique real root α^* which is the leading one for the asymptotic expansion of the solution of (8.53). Thus we have

$$j(t) \approx j(0) e^{\alpha^* t}.$$

We also know that α^* is positive if and only if

$$u_0 N \int_0^{+\infty} K(s) ds = R_0 u_0 > 1,$$

and we see that the usual threshold condition, involving the basic reproduction number R_0 , determines the epidemic outbreak with initial exponential growth at a rate α^* .

The age of infection

The models presented here, based on integro-differential equations, try to capture the effects due to the disease progression within the infected individual, both in what concerns the probability of recovering and the infectiousness. Though not explicitly expressed, the main variable, denoted by θ , is the age of the infection, i.e. the time elapsed since infection, and the state of the infected population can be described by

$$i(\theta, t)$$

denoting the distribution of the infected individuals with respect to θ .

This description is similar to that of a population structured by demographic age, as it was presented in Sect. 2.5. Actually, $i(\theta, t)$ is related to the incidence $j(t)$ through the formula

$$i(\theta, t) = \Pi(\theta)j(t - \theta),$$

where $j(t)$ satisfies its own eq. (8.46)-ii and is connected to the susceptible population variable $S(t)$. Thus, to describe the model in terms of the two variables $i(\theta, t)$, $S(t)$, one can adopt the system (compare with (2.39) in Problem 2.6)

$$\begin{cases} S'(t) = -\lambda(t)S(t) \\ \frac{\partial i}{\partial t}(\theta, t) + \frac{\partial i}{\partial \theta}(\theta, t) + \gamma(\theta)i(\theta, t) = 0, \\ i(0, t) = \lambda(t)S(t), \end{cases}$$

where $\lambda(t)$ is still the force of infection,

$$\lambda(t) = \frac{c}{N} \int_0^{\theta_+} \chi(\theta) \Pi(\theta) i(\theta, t) d\theta$$

and $\gamma(\theta)$ is the θ -specific removal rate, i.e. we have

$$\Pi(\theta) = e^{-\int_0^\theta \gamma(s) ds}.$$

The previous system is actually the model originally considered by Kermack and McKendrick in their seminal papers [10–12]. However, for a long time the attention of researchers has been focused on the simplified version (8.4) and only in recent years the Kermack-McKendrick model has been considered in its full potentiality.

8.7 Variable population

We now focus on the consequences of assuming non trivial demographic aspects and of their interaction with the disease dynamics. As already pointed out, a relevant feature of the framework considered in the previous models is that the total population is constant even though, by demographic mechanisms, the distribution of the population through the epidemiological classes may vary as a consequence of demographic dynamics. Now we consider the case in which the total population $N(t)$ may depend on time due to demography and to the effects of the disease.

The main questions studied are whether an infective disease can control a population, or even drive it to extinction.

As the simplest model in this context, we consider the case of a disease of type S-I-S coupled with Malthusian demography (compare with (8.35) and (8.37))

$$\begin{cases} S'(t) = \beta N(t) - \frac{\sigma}{N(t)} I(t) S(t) - \mu S(t) + \gamma I(t), \\ I'(t) = \frac{\sigma}{N(t)} I(t) S(t) - \mu I(t) - \gamma I(t) - \nu I(t), \end{cases} \quad (8.54)$$

with

$$N(t) = S(t) + I(t) \quad (8.55)$$

and with the initial condition $S(0) = S_0$, $I(0) = I_0$.

Models of this type were proposed as the HIV/AIDS epidemics started spreading in South Saharan Africa. The assumption of population exponential growth at rate $r = \beta - \mu > 0$ seemed a reasonable approximation (at least in a short-term perspective) and the main question in the analysis was whether the deaths caused by the disease could decrease population growth or even turn it into decrease. Indeed, the model includes an additional mortality ν of infected people.

For a disease like HIV-AIDS for which recovery is considered not possible, we would set $\gamma = 0$, turning the model into an SI type. Clearly the model lacks realism in several aspects (for instance, this model assumes exponentially distributed infection period, and constant infectiousness, in contrast with all known information), but it is a first step to assess the effect of disease on demography.

Another effect of the infection on demography could consist in the reduction of fertility of infected individuals (or even their complete sterilization); for the sake of simplicity, this is neglected here, but it would not be difficult adding such an effect to the model. Finally, vertical transmission (i.e., infection transmission from mother to child) occurs for several infections, and this effect could also be considered.

Using (8.55), from the equations we have

$$N'(t) = rN(t) - \nu I(t)$$

so that we need to keep the total population $N(t)$ as a variable of the problem and possibly discuss its influence on the force of infection (see (8.6)), though here we assume the contact rate c to be constant, so that $\sigma = c\chi$ is constant.

A convenient transformation of system (8.54) can be performed using the following state variables

$$N(t), \quad v(t) = \frac{I(t)}{N(t)}$$

with the constraint $0 \leq v(t) \leq 1$. In fact, using (8.54) we have

$$\begin{cases} v'(t) = (\sigma - \beta - \gamma - v) \left(1 - \frac{\sigma - v}{\sigma - \beta - \gamma - v} v(t) \right) v(t), \\ N'(t) = (r - v v(t)) N(t) \end{cases} \quad (8.56)$$

and the first equation is decoupled from the second. It is then easy to prove the following dichotomy:

Let $0 < v_0 \leq 1$, then $0 < v(t) \leq 1$ and:

- if $\sigma - v - \beta - \gamma < 0$, then $\lim_{t \rightarrow +\infty} v(t) = 0$;
- if $\sigma - v - \beta - \gamma > 0$, then $\lim_{t \rightarrow +\infty} v(t) = v^*$,

where

$$v^* = \frac{\sigma - \beta - \gamma - v}{\sigma - v}.$$

Note that $0 < v^* < 1$, since $\sigma - v - \beta - \gamma > 0$.

The condition for $v(t)$ to converge to a positive quantity can be interpreted through a modified reproduction number of the infection

$$R_1 = \frac{c\chi}{\beta + \gamma + v}. \quad (8.57)$$

R_1 is obtained by considering an infective introduced at time 0 in a completely susceptible population. Differently from the usual reproduction number, we argue in terms of fractions: the initial infective constitutes a fraction $1/N_0$ of the population, but as the total population is growing at rate r , $N(s) = N_0 e^{rs}$, a new infective produced at time s must be divided by the factor $N_0 e^{rs}$. In other words, the number of new infectives must be discounted by the factor e^{-rs} according to the time s when they are produced. As the probability of surviving as an infective to time s is $e^{-(\mu+v+\gamma)s}$ and the rate at which new infectives are produced is $c\chi$, we obtain

$$R_1 = \int_0^{+\infty} c\chi e^{-rs} e^{-(\mu+v+\gamma)s} ds = \frac{c\chi}{\beta + v + \gamma}.$$

The previous result accounts for conditions for the disease to become endemic with a constant fraction v^* of infectives. In this case, from the second equation in (8.56) we can determine the eventual behavior of the population. In fact the popula-

tion will eventually growth at a rate

$$r^* = r - \nu v^*.$$

If $R_1 < 1$, then $v(t) \rightarrow 0$, and the population as a whole will grow at rate r . It is still possible that the infectives, while approaching 0 as fraction of the population, go to infinity.

Indeed, looking at the second of (8.54), we see that, since, as $t \rightarrow \infty$, $v(t) \rightarrow 0$ so that $S(t)/N(t) \rightarrow 1$, it is asymptotic to the linear equation

$$I'(t) = (\sigma - \mu - \gamma - \nu)I(t). \quad (8.58)$$

Hence $I(t)$ grows to infinity if

$$R_0 = \frac{\sigma}{\mu + \gamma + \nu} > 1,$$

and decreases to 0 if $R_0 < 1$. Here, R_0 is the usual basic reproduction number of the infection, counting the average number of new infectives generated by one infective in a totally susceptible population.

Concluding we have:

- if $R_0 < 1$, then
 $N(t)$ grows exponentially at rate r , $\lim_{t \rightarrow +\infty} I(t) = 0$;
- if $R_0 > 1 > R_1$, then
 $N(t)$ grows exponentially at rate r , $\lim_{t \rightarrow +\infty} I(t) = +\infty$, $\lim_{t \rightarrow +\infty} v(t) = 0$;
- if $R_1 > 1$, then
 $N(t)$ grows (or decreases) exponentially at rate $r^* = (r - \nu v^*)$,
 $\lim_{t \rightarrow +\infty} v(t) = v^*$.

We then see that an infectious disease can decrease the rate of exponential growth of a population, or even drive it to extinction. This can occur only if $\nu > r = b - \mu$; in that case the infected fraction v^* must be large enough so that $r^* > 0$.

The previous S-I-S model (8.54) can be extended to include other features, such as non-linear demographic dynamics and contact rates depending on population size. This is considered in the following system

$$\begin{cases} S'(t) = \beta(N(t))N(t) - \frac{\sigma(N(t))}{N(t)}I(t)S(t) - \mu(N(t))S(t) + \gamma I(t), \\ I'(t) = \frac{\sigma(N(t))}{N(t)}I(t)S(t) - \mu(N(t))I(t) - \gamma I(t) - \nu I(t). \end{cases} \quad (8.59)$$

In (8.59) $N(t)$ is given by (8.55), the functions $\beta(N)$ and $\mu(N)$ are the demographic parameters as discussed in Chap. 1, γ and ν are the recovery rate and the disease in-

duced mortality respectively, $\sigma(N) = \chi c(N)$ where χ is the infectiousness and $c(N)$ the population dependent contact rate.

We consider the following assumptions:

- *demographic rates*

$$\beta'(N) < 0, \quad \mu'(N) > 0, \quad \text{there exists } K > 0 \quad \text{such that} \quad \beta(K) = \mu(K);$$

- *contact rate*

$$c(0) \geq 0, \quad c'(N) \geq 0, \quad \text{the function } N \rightarrow \frac{c(N)}{N} \quad \text{is non-increasing.}$$

The assumptions on the demographic rates amount to assume that the population, if disease free, follows a logistic model with growth rate $r(N) = \beta(N) - \mu(N)$ and carrying capacity K . The assumptions on $c(N)$ reflect the basic properties of a contact rate which increases with the population size but undergoes saturation when the population increases to infinity. A few specific forms of $c(N)$ have been proposed to meet different possible mechanisms, namely:

- **mass action:**

$$c(N) = c_0;$$

- **standard mass action:**

$$c(N) = c_0 N;$$

- **saturating:**

$$c(N) = \frac{c_0 N}{1 + kN};$$

- **empirical:**

$$c(N) = c_0 N^\alpha \quad \text{with} \quad \alpha \in (0.03, 0.07).$$

It may be natural asking for the property $c(0) = 0$, meaning that, as the population goes to 0, necessarily contacts go to 0. Such a property is not satisfied by the first example, which we used extensively so far; in models with constant total population size N , such as (8.4), it is clearly irrelevant asking what happens when N goes to 0. We will see that, in these deterministic models, population extinction caused by an infectious disease may occur only if $c(0) > 0$; therefore, in order to include this phenomenon, we ask only for $c(0) \geq 0$. A rigorous analysis of population extinction would definitely require a (much more complex) stochastic model, but the present models allows for a first assessment of the problem.

To study model (8.59), it is convenient to use, as before, the variables $N(t) = S(t) + I(t)$ and $v(t) = I(t)/N(t)$. In fact system (8.59) is equivalent to the system

$$\begin{cases} N'(t) = (\beta(N(t)) - \mu(N(t)) - v\nu(t))N(t) \\ v'(t) = ((\sigma(N(t)) - v)(1 - v(t)) - \gamma - \beta(N(t)))v(t). \end{cases} \quad (8.60)$$

This system is well posed, in the feasible invariant region $N \geq 0$, $0 \leq v \leq 1$ of the phase plane (N, v) . Here we can allow for $\sigma(\cdot)$ not Lipschitz in 0 as in the case of the *empirical* form for the contact rate $c(N)$ (see problem 8.2),

The two equilibria with $v = 0$ are immediate to identify:

$$E_0 \equiv (0, 0), \quad F \equiv (K, 0)$$

i.e. the *empty equilibrium* and the *disease free* one. Their Jacobians are, respectively,

$$J(E_0) = \begin{pmatrix} \beta(0) - \mu(0) & 0 \\ 0 & \sigma(0) - \beta(0) - \gamma - v \end{pmatrix}$$

and

$$J(F) = \begin{pmatrix} (\beta'(K) - \mu'(K))K & -vK \\ 0 & \sigma(K) - \beta(K) - \gamma - v \end{pmatrix}.$$

The eigenvalues of $J(E_0)$ and $J(F)$ are their diagonal elements, as the matrices are triangular. As $\beta(0) > \mu(0)$, the empty equilibrium is always unstable. The disease free equilibrium, instead, is unstable (remember $\beta(K) = \mu(K)$) if

$$R_0 = \frac{\sigma(K)}{\mu(K) + \gamma + v} > 1 \quad (8.61)$$

where R_0 represents the basic reproduction number at the carrying capacity. This condition means that the disease-free equilibrium is unstable if an infected introduced into a susceptible population at the carrying capacity would on average produce more than one infected.

We wonder whether *extinction* equilibria of the type $E_1 = (0, \hat{v})$ could exist. Looking at the second of (8.60), we find

$$\hat{v} = 1 - \frac{\gamma + \beta(0)}{\sigma(0) - v} = \frac{\sigma(0) - v - \gamma - \beta(0)}{\sigma(0) - v} \quad (8.62)$$

which is feasible (i.e. $0 < \hat{v} < 1$) if and only if

$$R_1 = \frac{\sigma(0)}{v + \gamma + \beta(0)} > 1 \quad (8.63)$$

(compare (8.57)).

The Jacobian at E_1 is

$$J(E_1) = \begin{pmatrix} \beta(0) - \mu(0) - v\hat{v} & 0 \\ (\sigma'(0) - \beta'(0))\hat{v} & \sigma(0) - v - \gamma - \beta(0) \end{pmatrix}.$$

Again the eigenvalues of $J(E_1)$ are its diagonal elements. Because of (8.63), E_1 is asymptotically stable or unstable according to whether the parameter

$$\hat{r} = \beta(0) - \mu(0) - \nu\hat{v}$$

is negative or positive.

To complete the analysis, we should look for *endemic equilibria* (N^*, v^*) . To this purpose, also with the aim of understanding global behavior, it is convenient to look at the isoclines

$$v = \frac{\beta(N) - \mu(N)}{\nu} := \phi_1(N) \quad \text{and} \quad v = 1 - \frac{\gamma + \beta(N)}{\sigma(N) - \nu} := \phi_2(N).$$

From the assumptions on demographic and contact rates, it is clear that $\phi_1(\cdot)$ is a decreasing function, while $\phi_2(\cdot)$ is increasing in the set

$$\mathcal{R} = \{N : \sigma(N) \geq \nu + \gamma + \beta(N)\} = [N_+, +\infty)$$

where $\phi_2(N) \in [0, 1]$. Hence there is *at most* one intersection between the two isoclines, i.e. at most one endemic equilibrium. Note that we look for such intersection in the set \mathcal{R} because it must be $0 < v^* < 1$.

We can also see that this endemic state $E^* = (N^*, v^*)$ is stable whenever it exists. In fact the Jacobian at E^* reads

$$J(E^*) = \begin{pmatrix} (\beta'(N^*) - \mu'(N^*))N^* & -\nu N^* \\ (\sigma'(N^*) - \beta'(N^*))v^* & -(\sigma(N^*) - \nu)v^* \end{pmatrix}$$

and we have

$$\text{trace } J(E^*) = (\beta'(N^*) - \mu'(N^*))N^* - (\sigma(N^*) - \nu)v^* < 0,$$

$$\det J(E^*) = v^* N^* ((\sigma(N^*) - \nu)(\mu'(N^*) - \beta'(N^*)) + \nu(\sigma'(N^*) - \beta'(N^*))) > 0,$$

where we have used $\sigma(N^*) > \nu$ which holds because $N^* \in \mathcal{R}$.

More specifically, looking at the phase plane (N, v) , there are four possible cases, corresponding to the four panels of Fig. 8.19, but the two curves intersect in \mathcal{R} only when the following two conditions are both satisfied

$$\phi_1(0) > \phi_2(0) \tag{8.64}$$

$$K \in \mathcal{R} \tag{8.65}$$

i.e. in the two cases (b) and (c) of Fig. 8.19.

We note that, when $R_1 > 1$ and the equilibrium E_1 exists, condition (8.64) is equivalent to

$$\hat{r} = \beta(0) - \mu(0) - \nu\hat{v} > 0.$$

Also, when $R_0 > 1$, then (8.65) is satisfied.

Hence, referring to Fig. 8.19 and recalling that $R_1 < R_0$, we can summarise the cases in the following scenario:

- $R_1 < R_0 < 1$ (panel a)
neither E_1 nor E^* exist, and the disease-free equilibrium F is globally attractive;
- $R_1 < 1 < R_0$ (panel b)
 E_1 does not exist, F is unstable, E^* exists and is globally attractive;
- $1 < R_1 < R_0$ and $\hat{r} = \beta(0) - \mu(0) - v\hat{v} > 0$ (panel c)
 F is unstable, both E_1 and E^* exist but E_1 is unstable while E^* is asymptotically stable and globally attractive;
- $1 < R_1 < R_0$ and $\hat{r} = \beta(0) - \mu(0) - v\hat{v} < 0$ (panel d)
 F is unstable, only the extinction equilibrium E_1 exists and is asymptotically stable; consideration of the phase plane shows that E_1 is globally attractive.

A few comments are now in order concerning what the previous analysis tells about the interactions between infection and demography.

First of all, we see that infection persistence depend on the basic reproduction number R_0 given by (8.61), i.e. computed in a totally susceptible population at the demographic equilibrium K .

Second, we have seen that population extinction caused by an infectious disease can occur only if $c(0) > 0$, and requires rather stringent conditions on the parameter values.

The value $c(0)$ can only be considered as a limiting value: the limit of contact rate as the population becomes very low; however, when the population is very low, a model accounting for the discrete nature of populations seems necessary for a precise analysis. These computations however suggest that extinction caused by a pathogen agent can occur only if contacts remain high even at very low population densities, which is unlikely for airborne infections, but may be possible in particular cases.

The situation would be different if the pathogen can be transmitted also through alternative host species. Then it would be possible that one species is driven to extinction by a lethal pathogen, that goes being maintained in another species, especially when the demography of that species is hardly affected by the pathogen. This resemble what happens for predators: it is very unlikely that a specialist predator drives its only prey species to extinction, while this is possible for a generalist predator (see the section on 2 prey-1 predator).

A final point concerns the differences between the effect of predators and pathogens. As we have seen above, a simple host-pathogen model always converge to an equilibrium, while we saw that simple predator-prey systems can give rise to oscillations. This depends on the specific bilinear form generally used for modeling infection transmission.

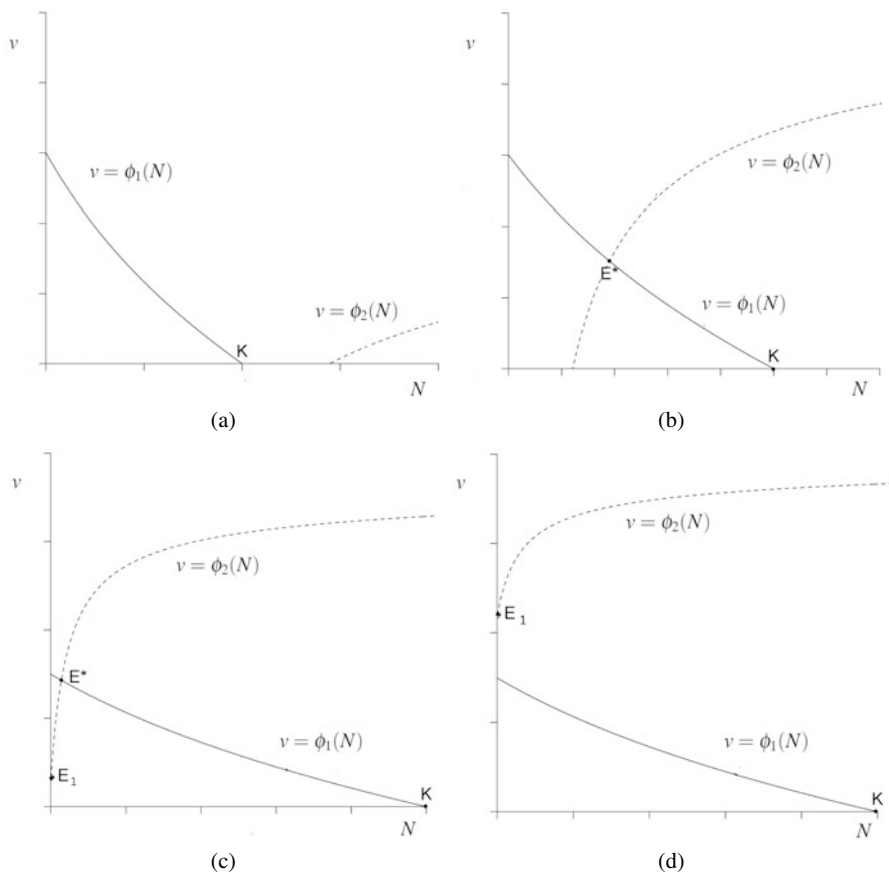


Fig. 8.19 The isoclines of system (8.60) in 4 different configurations. See text for details

8.8 Heterogeneity in contacts

In the previous sections, we have assumed that the population is homogeneously mixing, in the sense that at any time each individual has the same probability of contacting any other individual, independently of previous contacts.

We know however that individuals form networks of contacts, depending for instance on belonging to the same family, attending the same school or the same class, being friends or work collaborators, so that infection transmission happens preferentially through these paths.

Recognizing these factors and thanks to the advancement of computing power, in the last decade several research groups have modeled infection spread, by realizing software tools that build synthetic populations with contact networks that attempt to reproduce several quantitative properties of actual contact networks, as available from several sources of data. Simulations of infection spread through these networks

can then be studied to identify features brought by the network structure, and compare them to data from actual epidemics.

When the network structure is particularly simple, for instance consisting only of households, each grouping together a certain number of individuals that mix homogeneously within the household as a given rate, while contacting all other members of the population at the same lower rate, it is possible also to obtain analytic results. Such models are necessarily stochastic, as the number of individuals in each household is small, so that infection transmission in a household cannot be modeled as a deterministic process.

Here we present instead a simpler modeling approach, which still yield some insights on the effect of heterogeneities in contact rates on infection spread. Instead of attempting to reproduce actual contact network, we focus on some specific factor (for instance age, or location in space) that affects contacts; it is clear, for instance, that residents of one village will be more likely to transmit an infection between each other than to somebody who lives far away. Similarly, it is known that contact rates are higher among individuals of the same age (especially if it is a school-age). Thus, the population will be partitioned in a (small) number of groups, each considered homogeneously mixing within, and differential equations for the fraction of susceptible, infected, removed individuals in each group are obtained, as shown below.

Let us divide the population into n groups and denote by

$$S_i(t), I_i(t), R_i(t), i = 1, \dots, n$$

the number of susceptibles, infectives and removed in each group, whose total density is $N_i(t) = S_i(t) + I_i(t) + R_i(t)$. We need to model contacts of each group with any other, thus we introduce:

- c_i : total contact rate of individuals belonging to group i ;
- q_{ij} : the fraction of those contacts that occur with individuals of group j .

We will assume both c_i and q_{ij} constant, though, as in the previous sections, in a more general model they could be assumed depending on t . As contacts are reciprocal, the components of the vector $\mathbf{c} \equiv (c_1, \dots, c_n)$ and the entries of the matrix $\mathbf{q} \equiv ((q_{ij}), i, j = 1, \dots, n)$, cannot be totally arbitrary. The total number of contacts that group i has with group j , must be equal to the number of contacts that group j has with group i , namely we have the constraint

$$N_i(t)c_iq_{ij} = N_j(t)c_jq_{ji} \quad \forall i, j = 1, \dots, n. \quad (8.66)$$

Then, we can build the infection rate (force of infection) $\lambda_i(t)$ for each group i . In fact the probability that a susceptible of group i gets infected in the interval $(t, t + \Delta t)$ is the sum over all groups j (including i itself) of the probabilities of getting infected by an infective of group j ; this latter is equal to the probability of contacting a j -individual in the interval (in first approximation $c_i \Delta t q_{ij}$) times the probability that the individual is infective ($I_j(t)/N_j(t)$) times the probability of infection per contact

(χ); hence $\chi c_i \Delta t q_{ij} I_j(t) / N_j(t)$. Thus we obtain the average number of individuals of group i getting infected in the unit time

$$\lambda_i(t) = \chi c_i \sum_{j=1}^n q_{ij} \frac{I_j(t)}{N_j(t)}. \quad (8.67)$$

Any of the previous epidemic models could be analyzed with the law (8.67) for the force of infection exerted on group i .

We will limit ourselves to present some results concerning the SIR model with demography and without disease-induced mortality. Namely we extend model (8.36) of Sect. 8.4 to the case of n groups. Standard assumptions are then that population density of each group N_i is constant and that the ‘natural’ mortality rate μ_i is exactly balanced by an entrance rate $\Lambda_i = \mu_i N_i$. Letting γ be the recovery rate, one arrives at the system of equations

$$\begin{cases} S'_i(t) = \Lambda_i - S_i(t) \sum_{j=1}^n \frac{\beta_{ij}}{N_j} I_j(t) - \mu_i S_i(t) \\ I'_i(t) = S_i(t) \sum_{j=1}^n \frac{\beta_{ij}}{N_j} I_j(t) - (\mu_i + \gamma) I_i(t) \end{cases} \quad (8.68)$$

where we set

$$\beta_{ij} = \chi c_i q_{ij}. \quad (8.69)$$

Actually, system (8.68) can be conveniently rescaled using the susceptibles and infectives fractions

$$u_i(t) = \frac{S_i(t)}{N_i}, \quad v_i(t) = \frac{I_i(t)}{N_i}.$$

In fact we have

$$\begin{cases} u'_i(t) = \mu_i(1 - u_i(t)) - u_i(t) \sum_{j=1}^n \beta_{ij} v_j(t) \\ v'_i(t) = u_i(t) \sum_{j=1}^n \beta_{ij} v_j(t) - (\mu_i + \gamma) v_i(t) \end{cases}. \quad (8.70)$$

where the parameters keep their dimensions. Of course we still have to give constitutive forms to c_i and q_{ij} that may follow from the modeling arguments discussed in the previous sections. We will first focus on the analysis of a simple case that yields itself to a simple and complete analysis and fits with the demographic assumptions above, leading to constant N_i .

Precisely, let us consider the case where the contact rates c_i are constant and the fraction of contacts q_{ij} is based on the so-called *proportionate mixing*, i.e. we assume that the fraction of contacts that individuals of any given group i have with individuals of group j is proportional to the ‘offer’ of contacts from group j , i.e.

$$q_{ij} = \frac{c_j N_j}{\sum_{k=1}^n c_k N_k}.$$

It can be observed that this rule immediately satisfies the constraints (8.66).

With the assumptions above the coefficients (8.69) are constant and take the form

$$\beta_{ij} = a_i b_j, \quad (8.71)$$

where

$$a_i = \chi c_i, \quad b_i = \frac{c_i N_j}{\sum_{k=1}^n c_k N_k}. \quad (8.72)$$

Actually the form (8.71), named *separable kernel*, may occur also with assumptions other than those of the proportionate mixing case (8.72) and we assume this form to analyze model (8.70).

Substituting (8.71) in (8.70) and, to simplify the computations, assuming also that mortality is the same in all groups ($\mu_i \equiv \mu$), we arrive at

$$\begin{cases} u'_i(t) = \mu (1 - u_i(t)) - a_i u_i(t) \sum_{j=1}^n b_j v_j(t) \\ v'_i(t) = a_i u_i(t) \sum_{j=1}^n b_j v_j(t) - (\mu + \gamma) v_i(t). \end{cases} \quad (8.73)$$

It is clear that system (8.73) has the infection-free equilibrium, where $u_i = 1$ and $v_i = 0$ for each $i = 1 \dots n$, i.e. $E_0 \equiv (1, \dots, 1, 0, \dots, 0)$. The stability of E_0 can be studied by linearizing (8.73) at E_0 . The corresponding Jacobian is a block-triangular ($2n \times 2n$) matrix

$$J(E_0) = \begin{pmatrix} -\mu I & -B \\ 0 & B - (\mu + \gamma)I \end{pmatrix} \quad (8.74)$$

where the entries of the $(n \times n)$ matrix B are $B_{ij} = a_i b_j$.

As $J(E_0)$ is block-triangular, its eigenvalues are the eigenvalues of $-\mu I$ (i.e. only $-\mu$) and the eigenvalues of $B - (\mu + \gamma)I$. Hence:

E_0 is asymptotically stable if all the eigenvalues of $B - (\mu + \gamma)I$ have negative real part.

Actually, the eigenvalues can be easily computed as follows.

First of all, λ is an eigenvalue of $B - (\mu + \gamma)I$ if and only if $\lambda + (\mu + \gamma)$ is an eigenvalue of B . We can then look for eigenvalues of B and subtract $\mu + \gamma$.

Concerning B , if λ is an eigenvalue and $\mathbf{x} \equiv (x_1, \dots, x_n)$ is the corresponding eigenvector, then

$$\lambda x_i = a_i \sum_{j=1}^n b_j x_j \quad i = 1 \dots n, \quad (8.75)$$

and, since \mathbf{x} is not trivial, we must have $\sum_{j=1}^n b_j x_j \neq 0$. Since \mathbf{x} is determined but for a multiplicative constant, we can choose $\sum_{j=1}^n b_j x_j = 1$, so that (8.75) becomes

$$\lambda x_i = a_i, \quad i = 1, \dots, n.$$

Finally, multiplying the latter equation times b_i and summing for i from 1 to n , one obtains

$$\lambda \sum_{i=1}^n b_i x_i = \sum_{i=1}^n a_i b_i.$$

i.e.

$$\lambda = \sum_{i=1}^n a_i b_i = \sum_{i=1}^n \beta_{ii}. \quad (8.76)$$

Thus we see that B has only one eigenvalue given by (8.76) and from the previous considerations on the eigenvalues of $J(E_0)$ we conclude:

- if $\sum_{i=1}^n a_i b_i = \sum_{i=1}^n \beta_{ii} < \mu + \gamma$ then the infection-free equilibrium E_0 is asymptotically stable;
- if $\sum_{i=1}^n a_i b_i = \sum_{i=1}^n \beta_{ii} > \mu + \gamma$ it is unstable.

It is not difficult to show that the asymptotic stability is indeed global. First of all, note that the set $\{0 \leq u_i, v_i, 0 \leq u_i + v_i \leq 1, i = 1 \dots n\}$ is an invariant set for (8.73) that contains all biologically relevant solutions. Then consider the function

$$V(u_1, \dots, u_n, v_1, \dots, v_n) = \sum_{i=1}^n b_i v_i.$$

Computing its derivative along the solutions of (8.73) and using the inequality $u_i \leq 1$, one finds

$$\dot{V} = \left(\sum_{i=1}^n a_i b_i u_i - (\mu + \gamma) \right) V \leq \left(\sum_{i=1}^n a_i b_i - (\mu + \gamma) \right) V < 0.$$

V is thus a Lyapunov function for system (8.73). By La Salle Theorem (see Appendix A), all solutions must converge to the set where $\dot{V} = 0$, i.e. where $V = 0$, i.e. where $v_i = 0$ for all $i = 1 \dots n$.

As for the components u_i , system (8.73) restricted to the set $\{u_i = 0, i = 1 \dots n\}$, becomes

$$u_i'(t) = \mu(1 - u_i(t)),$$

whose only stable equilibrium is $\{u_i = 1, i = 1 \dots n\}$.

When the disease free equilibrium E_0 is unstable, existence of endemic equilibria (u_i^*, v_i^*) , $i = 1 \dots n$ of (8.73) occurs. Indeed, to look for such equilibria we have to solve the system

$$\begin{cases} \mu(1 - u_i^*) - a_i u_i^* \sum_{j=1}^n b_j v_j^* = 0 \\ a_i u_i^* \sum_{j=1}^n b_j v_j^* - (\mu + \gamma) v_i^* = 0. \end{cases} \quad (8.77)$$

Setting $A^* = \sum_{j=1}^n b_j v_j^*$, from the first of (8.77) we obtain

$$u_i^* = \frac{\mu}{\mu + a_i A^*}$$

and from the second

$$v_i^* = \frac{a_i u_i^* A^*}{\mu + \gamma} = \frac{a_i A^* \mu}{(\mu + \gamma)(\mu + a_i A^*)}. \quad (8.78)$$

Notice that

$$u_i^* + v_i^* < \frac{\mu}{\mu + a_i A^*} + \frac{a_i A^*}{\mu + a_i A^*} = 1$$

hence, given any $A^* > 0$, the previous formulae yield feasible values for (u_i^*, v_i^*) .

We still have to find possible values for A^* . Multiplying (8.78) times b_i , we get

$$A^* = \sum_{i=1}^n b_i v_i^* = \sum_{i=1}^n \frac{a_i b_i A^* \mu}{(\mu + \gamma)(\mu + a_i A^*)}.$$

Since A^* must be strictly positive, otherwise we would have $v_i = 0$ for $i = 1, \dots, n$, we can divide both sides by A^* and find that A^* must solve $F(A^*) = 1$ with

$$F(A) = \sum_{i=1}^n \frac{a_i b_i \mu}{(\mu + \gamma)(\mu + a_i A)}. \quad (8.79)$$

It is immediate to see that F is a decreasing function with $\lim_{A \rightarrow \infty} F(A) = 0$. Hence the equation $F(A) = 1$ has a positive solution if and only if $F(0) > 1$. Thus we have the following threshold result:

the multi-group system with separable kernel has a (unique) endemic equilibrium if and only if

$$\sum_{i=1}^n a_i b_i = \sum_{i=1}^n \beta_{ii} > (\mu + \gamma) \quad (8.80)$$

and we find the same condition for the instability of E_0 .

Concerning stability of this equilibrium it is possible to obtain a rather complete results and show that it is globally asymptotically stable. Actually such results can be obtained for the general system (8.68) by more delicate arguments involving the use of Lyapunov functions. We refer to [13] and [6] for proofs and details.

8.9 The general multi-site model and the next generation matrix

We have found that (8.80) acts as a threshold condition. When the inverse inequality is satisfied, the disease-free equilibrium is asymptotically stable, and there is no endemic equilibrium; if instead condition (8.80) is fulfilled, the disease-free equilibrium is unstable, and there exists a unique endemic equilibrium. In the other cases

considered in this chapter, we have related existence and stability of endemic states to a reproduction number R_0 , that corresponds to the average number of individuals infected by one infective, over all the course of the infection, in a completely susceptible population. In the present situation, with many groups exchanging contacts and infecting each other, it is not straightforward to summarize the infection process in one basic number acting as a threshold parameter and having a meaning in terms of the effect that one single infective produces in the population.

Actually, a definition of reproduction number for epidemics, in very general contexts, was introduced by Diekmann et al. in [4] and became almost universally accepted. We will present the concept in the context of system (8.68), which is more limited than what can be addressed, but (we believe) is sufficient to illustrate the main ideas.

The problem with the definition of a basic reproduction number in a multi-group setting is that the initial infective could belong to any group, as well as the new infected. Thus, this definition is not related to a number but to a matrix K , named *the next-generation matrix*, whose entries K_{ij} represent the average number of individuals of the group i infected by an infective, initially belonging to the group j , over the course of the infection.

In the case of the general system (8.68), we have

$$K_{ij} = \frac{N_i \beta_{ij}}{N_j (\mu_j + \gamma)}.$$

In fact K_{ij} can be computed multiplying the rate $(N_i \beta_{ij}/N_j)$ at which the N_i susceptibles in group i are infected by one infective of the N_j individuals belonging to group j , by the mean length $((\mu_j + \gamma)^{-1})$ of the infectious period in group j . The word ‘initially’ in the clause ‘initially belonging to the group j ’ is pleonastic in this context, as we assumed that individuals cannot change group, but it will be helpful for generalizations.

We note that, thanks to the constraint (8.66) we have

$$K_{ij} = \frac{\beta_{ji}}{(\mu_j + \gamma)}. \quad (8.81)$$

Now, if we initially introduce a vector $\mathbf{v}_0 = (v_1, \dots, v_n)$ of infectives, from the definition of K , we see that they will, on average, produce the vector $\mathbf{v}_1 = K\mathbf{v}_0$ of new infectives. Each of these “new” infectives will on turn produce other infectives according to the same rule (as long as the infected number is low enough to neglect the decrease in susceptibles) yielding the vector $\mathbf{v}_2 = K^2\mathbf{v}_0$ of ‘secondary’ infections; and so on. Neglecting susceptible depletion at each step, the n -th generation of infectives will be $\mathbf{v}_n = K^n\mathbf{v}_0$, i.e. the solution of the discrete equation

$$\mathbf{v}_{n+1} = K\mathbf{v}_n.$$

Now, we know (see Appendix C) that the asymptotic behavior (for $n \rightarrow \infty$) of $\mathbf{v}_n = K^n\mathbf{v}_0$ is determined by the spectral radius of K , i.e. by

$$\rho(K) = \max_{i=1 \dots n} |\lambda_i| = \lim_{n \rightarrow \infty} \|K^n\|^{1/n}.$$

In fact we expect to have

$$\mathbf{v}_n \approx \rho^n(K) \mathbf{e}_0 \quad \text{hence} \quad \mathbf{v}_{n+1} \approx \rho(K) \mathbf{v}_n,$$

where \mathbf{e}_0 is the projection of \mathbf{v}_0 on the eigenvector corresponding to the leading eigenvalue. Hence it is natural to give the following definition:

in a multigroup epidemic, the basic reproduction ratio R_0 is defined at the spectral radius of the next-generation matrix K :

$$R_0 = \rho(K).$$

The previous definition may look to be based on inconsistent assumptions as, on the one hand, we neglect susceptible depletion, making an approximation valid only at the start of an epidemic; on the other hand, we consider the limit for $n \rightarrow \infty$, thus asking for many generations of infectives. It can, however, be proved rigorously that it yields a threshold for epidemic onset. Indeed the following result holds:

the disease-free equilibrium of (8.68) is asymptotically stable if $R_0 < 1$; it is unstable if $R_0 > 1$.

The proof is based on the following result (see for instance [10], Theorem 8.15):

let B a non-negative matrix and M a nonsingular M -matrix. Let $s(B - M)$ the spectral bound of $B - M$. Then

$$s(B - M) < 0 \iff \rho(BM^{-1}) < 1. \quad (8.82)$$

Indeed, it is clear that (8.68) has the disease-free equilibrium

$$E_0 \equiv (1, \dots, 1, 0, \dots, 0).$$

Then we have the Jacobian

$$J(E_0) = \begin{pmatrix} -M & -B \\ 0 & B - D \end{pmatrix} \quad (8.83)$$

where the $(n \times n)$ matrices M , B and D are

$$M = \text{diag} \begin{pmatrix} \mu_1 \\ \vdots \\ \mu_n \end{pmatrix}, \quad B \equiv ((\beta_{ij})), \quad D = M + \gamma I.$$

As in the analysis of (8.74), $J(E_0)$ is block-triangular, hence its eigenvalues are the eigenvalues of $-M$ (i.e. its diagonal elements, all negative) and the eigenvalues of $B - D$. Hence E_0 is asymptotically stable if all the eigenvalues of $B - D$ have neg-

ative real part. Since D is a diagonal matrix with all positive elements, we can apply the quoted result and obtain that:

the disease-free equilibrium E_0 is asymptotically stable (resp. unstable) if

$$R_0 = \rho(K) = \rho(BD^{-1}) < 1 \quad (\text{resp. } > 1). \quad (8.84)$$

It should be clear that the same result can be applied to much more general scenarios than (8.68), as can be seen in [4].

In the case of model (8.73) (i.e. with the separable kernel (8.71) and $\mu_i = \mu$) we have (see (8.81) and (8.71))

$$K_{ij} = \frac{a_j b_i}{\mu + \gamma}$$

and it can be seen that (Problem 8.10)

$$R_0 = \rho(K) = \frac{1}{\mu + \gamma} \sum_{i=1}^n a_i b_i = \frac{1}{\mu + \gamma} \sum_{i=1}^n \beta_{ii},$$

and the result stated in (8.80) matches with (8.84).

Finally, in the particular case of the proportionate mixing assumption, when the coefficients β_{ij} are given by (8.72), we have

$$R_0 = \frac{1}{\mu + \gamma} \sum_{i=1}^n a_i b_i = \frac{\chi}{\gamma + \mu} \frac{\sum_{i=1}^n c_i^2 N_i}{\sum_{i=1}^n c_i N_i} = \frac{\chi}{\gamma + \mu} \frac{\sum_{i=1}^n c_i^2 \frac{N_i}{N}}{\sum_{i=1}^n c_i \frac{N_i}{N}} = \frac{\chi}{\gamma + \mu} \frac{\langle c^2 \rangle}{\langle c \rangle}$$

where $N = \sum_{j=1}^n N_j$ is the total population, and $\langle \cdot \rangle$ represents the average value of the discrete variable in the argument, with respect to the probabilities N_i/N .

We thus see that R_0 has an expression similar to what we found in the case of a homogeneous population, except for the fact that instead of the (homogeneous) contact rate c , here we have the ratio $\frac{\langle c^2 \rangle}{\langle c \rangle}$. This formula can be made more expressive by writing it in terms of the variance of c : $V[c] = \langle c^2 \rangle - \langle c \rangle^2$. In fact we have that:

in a population divided in groups, differing in contact rate, if the mixing is proportionate then

$$R_0 = \frac{\chi}{\gamma + \mu} \left(\langle c \rangle + \frac{V(c)}{\langle c \rangle} \right). \quad (8.85)$$

Formula (8.85) shows that R_0 cannot be determined in terms of the average contact rate, but one has to take also the variance into account. This fact has been rediscovered in the last decade in terms of epidemics on scale-free networks.

Problems

8.1. Technical details for the basic model

Consider problem (8.9) of Sect. 8.2.

1. Prove well-posedness of the model, showing non-negativeness of $u(t)$, $v(t)$ and then of $w(t)$. Conclude for boundedness after proving $u(t) + v(t) + w(t) = 1$.
2. Prove that the function $H(z)$ defined in (8.22) has one and only one root in the interval $(0, u_0)$.
3. Use the La Salle function (8.42) to prove global attractiveness of the endemic equilibrium of model (8.39).

8.2. Well-posedness of the variable population model

Consider model (8.60) with any of the constitutive forms for $C(N)$.

1. Prove that for $M > 0$ sufficiently large, the rectangle $\{0 < N \leq M, \quad 0 \leq v \leq 1\}$ is invariant.
2. Conclude for well-posedness of the model for any of the constitutive forms of $C(N)$.
3. Is well-posedness invalidate in the case of the empirical form $C(N) = c_0 N^\alpha$ that is not Lipschitz continuous at $N = 0$?

8.3. Parameters in the SIR model - 1

Consider an infectious disease of *SIR* type with an average period of infectiousness of 7 days; assume that on average each individual contacts 3 different people per day, and that there is 10% probability that a susceptible, contacted by an infected, becomes susceptible. Assume that the initial population is 1.4 millions of susceptibles, that the initial number of infectives be extremely low, and that births and deaths can be neglected.

1. Determine the basic reproductive number R_0 .
2. Determine the number of infectives at the peak.
3. Determine the fraction of the population that should be vaccinated at the start of the epidemic to prevent its spread.
4. Approximate as well as you can the number of susceptibles at the end of the epidemic.

8.4. Parameters in the SIR model - 2

Answer the same questions of the previous exercise, assuming that the information available are about the average period of infectiousness (estimated to 7 days) and the doubling time (i.e. the time in which the number of new infectives double during the exponential phase) in the initial phase of the epidemic estimated to be 10 days. Again assume that the initial population is 1.4 millions of susceptibles, that the initial number of infectives be extremely low, and that births and deaths can be neglected.

8.5. Vaccination strategies

Consider the SIR model (8.36) and suppose that a vaccination strategy is designed, directed at random to all individuals. Thus the model is modified by introducing a term $-VS(t)$ in the first equation, where the parameter V denotes the rate at which susceptibles are vaccinated becoming immune.

1. Write the model and scale variables to get a convenient non-dimensional system.
2. Find equilibria discussing their existence as the parameter V varies.
3. Find the critical value for V in order to have eradication of the disease.
4. How are the effect of this strategy different from the *vaccination at birth* strategy?

8.6. An SIRS model

Let us assume that an infectious disease has a behavior of $S \rightarrow I \rightarrow R \rightarrow S$ type, i.e. infected individuals, once recovered, remain immune from the infection for some time (and can then be considered removed) but then become again susceptibles.

1. Write a model for the spread of an infectious disease of this type in a closed population, following the lines of the *SIR* model analyzed in class.
2. Find the equilibria of such model and study their local stability, according to parameter values.
3. Study the global behavior of the system. [Hint: it could be useful employing the function $(SI)^{-1}$ as a Bendixson-Dulac function.]

8.7. The SEIR model in a closed population

Consider an SEIR model in a closed population; in other words, we assume that newly infected individuals move to class E (exposed), members of which are not infectious; individuals in class E move to class I at rate v . For the rest, the model is as (8.4):

1. Write down the system of differential equations in the variables $(S(t), E(t), I(t))$ describing the model.
2. Write it down as an integral equation in the variable $j(t) = \beta S(t)I(t)$ representing the rate of new infections. Show that one can obtain

$$j(t) = S(t) \int_0^\infty A(\tau) j(t - \tau) d\tau$$

for an appropriate function $A(\tau)$, assuming that the model holds for all times $t \in \mathbb{R}$.

3. Following steps similar to those used for the *SIR* model, it is possible to prove that

$$\lim_{t \rightarrow \infty} I(t) = \lim_{t \rightarrow \infty} I(t) = 0.$$

Using this fact, find an equation that it satisfied by $S_\infty = \lim_{t \rightarrow \infty} S(t)$. Note that it will be the same as for the *SIR* model with the same definition of R_0 .

4. Show that, under the assumptions $I(0) \approx 0$, $E(0) \approx 0$, one can approximate (for t close to 0) the equations for $E(t)$ and $I(t)$ with the linear system

$$\frac{d}{dt} \begin{pmatrix} E(t) \\ I(t) \end{pmatrix} = A \begin{pmatrix} E(t) \\ I(t) \end{pmatrix} \text{ for an appropriate matrix } A.$$

Using this fact, find the rate r such that $I(t) \approx I_0 e^{rt}$ for small t .

5. Assume that a rate $r = 0.5 \text{ (weeks)}^{-1}$ of initial exponential increase is estimated from data. Estimate R_0 assuming that the infectious period lasts 1 week on average, and the incubation (the length of the period spent in the class E) 2 weeks. How does this compare with the estimate that would have been obtained using an SIR model in which the incubation period were ignored? And how with the estimate obtained using an SIR model but assuming that the infectious period lasts 3 weeks on average?

8.8. The SEIR model in an open population

Consider an $SEIR$ model in an open population (with births and deaths) in a similar framework as the SIR model. Find the equilibria of the system, discussing the conditions under which a positive equilibrium exists. Study the stability of the disease-free equilibrium, and write down the condition for its stability as $\mathcal{R}_0 < 1$ for an appropriately defined quantity \mathcal{R}_0 . Note that this quantity will differ (slightly) from that obtained for the SIR model, and interpret it anyway as the average number of new infections produced by a newly infected individual along her/his infectious period, assuming everybody else is susceptible.

8.9. The stochastic SIR model

Consider a Markov process modeling an SIR epidemic (with closed population) in which 1 infected is introduced in a population with 3 susceptibles.

1. Write down the infinitesimal transition rates.
2. Compute the probability that the epidemics ends after 0, 1, 2 or 3 new infections.
[Hint: sketch on a piece of paper all possible paths of infections and recoveries, and compute the probability of each path through the embedded jump Markov chain]

8.10. Heterogeneous mixing

Consider model (8.68) under the separable kernel assumption (8.71).

1. Find the contact matrix $K \equiv (K_{ij})$ defined in (8.81) and, computing the eigenvalues, determine R_0 as the spectral radius of K .

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Models with several species and trophic levels

When the last glow-worm had dragged his frosty emerald lantern to bed over the hills of moss, and the sun rose, the wall was taken over by the next set of inhabitants. Here it was more difficult to differentiate between the prey and the predators, for everything seemed to feed indiscriminately off everything else. Thus the hunting wasps searched out caterpillars and spiders; the spiders hunted for flies; the dragon-flies, big, brittle, and hunting-pink, fed off the spiders and the flies; and the swift, lithe, and multicoloured wall lizards fed off everything

Gerald Durrell, "The World in a Wall"
in "My Family and Other Animals", 1956

The *interspecific competition* and *predation* models for two species interaction, presented in Chaps. 6 and 7, can be used as building blocks for designing more general mechanisms and ecosystems. Moving beyond the two species framework, we are led to consider non-planar systems and we meet systems that are mathematically more complex, possibly requiring specific treatment and analysis, and provide new insights into ecological dynamics. Even though we will not aim to a complete description of the World in a Wall, this chapter is devoted to a few cases of three species dynamics that illustrate some complexities of multiple species interaction and introduce to the use of some more advanced mathematical technique.

9.1 A case of non transitive competition

Here we consider a 3-species competition model that extends the 2-species Lotka-Volterra system of Sect. 7.9:

$$\begin{cases} N_1'(t) = r_1 \left(1 - \frac{N_1(t)}{K_1} - \alpha_{12} \frac{N_2(t)}{K_1} - \alpha_{13} \frac{N_3(t)}{K_1} \right), \\ N_2'(t) = r_2 \left(1 - \alpha_{21} \frac{N_1(t)}{K_2} - \frac{N_2(t)}{K_2} - \alpha_{23} \frac{N_3(t)}{K_2} \right), \\ N_3'(t) = r_3 \left(1 - \alpha_{31} \frac{N_1(t)}{K_3} - \alpha_{32} \frac{N_2(t)}{K_3} - \frac{N_3(t)}{K_3} \right). \end{cases} \quad (9.1)$$

We are interested in the so called *cyclical competition* case, where in the reduced dynamics (i.e. when one of the species is absent) Species 1 out-competes Species 2,

Species 2 out-competes Species 3 and Species 3 out-competes Species 1. Other cases are simpler and do not lead to unexpected dynamical behavior.

Following May and Leonard in [8], we add the following special symmetry assumptions that allow for simple computations

$$r_1 = r_2 = r_3 = r$$

$$\alpha_{12} \frac{K_2}{K_1} = \alpha_{23} \frac{K_3}{K_2} = \alpha_{31} \frac{K_1}{K_3} = \alpha < 1$$

$$\alpha_{21} \frac{K_1}{K_2} = \alpha_{32} \frac{K_2}{K_3} = \alpha_{13} \frac{K_3}{K_1} = \beta > 1.$$

After scaling the variables by the transformations

$$t \rightarrow \tilde{t} = rt, \quad N_i \rightarrow u_i = \frac{N_i}{K_i},$$

we finally get the system

$$\begin{cases} u_1'(t) = (1 - u_1(t) - \alpha u_2(t) - \beta u_3(t)) u_1(t), \\ u_2'(t) = (1 - \beta u_1(t) - u_2(t) - \alpha u_3(t)) u_2(t), \\ u_3'(t) = (1 - \alpha u_1(t) - \beta u_2(t) - u_3(t)) u_3(t), \end{cases} \quad (9.2)$$

with the key assumption

$$\alpha < 1 < \beta.$$

As usual we note that the model is well posed since the solutions are non-negative and bounded (see Chap. 7). Concerning equilibria, there exist the extinction equilibrium $E_0 \equiv (0, 0, 0)$, three exclusion equilibria

$$E_1 = (1, 0, 0), \quad E_2 = (0, 1, 0), \quad E_3 = (0, 0, 1),$$

and a coexistence equilibrium

$$E^* = \frac{1}{1 + \alpha + \beta} (1, 1, 1).$$

Now, E_0 is an unstable node since

$$J(E_0) = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix}.$$

Considering E_1 , we have

$$J(E_1) = \begin{pmatrix} -1 & -\alpha & -\beta \\ 0 & 1 - \beta & 0 \\ 0 & 0 & 1 - \alpha \end{pmatrix},$$

with eigenvalues $\lambda_1 = -1$, $\lambda_2 = 1 - \beta < 0$, $\lambda_3 = 1 - \alpha > 0$. Thus we see that E_1 is a saddle point.

If we reduce the system to a two dimensional system in the phase plane (u_1, u_3) (the case without species 2)

$$\begin{cases} u_1'(t) = (1 - u_1(t) - \beta u_3(t)) u_1(t), \\ u_3'(t) = (1 - \alpha u_1(t) - u_3(t)) u_3(t), \end{cases}$$

then the point $(1, 0)$ (corresponding to E_1 in the three-dimensional setting), is a saddle point with the axis u_1 as the stable manifold, while the unstable manifold is an orbit \mathcal{C}_1 connecting $(1, 0)$ with $(0, 1)$ (corresponding to E_3). In the three-dimensional setting of the phase plane (u_1, u_2, u_3) , the curve \mathcal{C}_1 is the orbit of a trajectory $\mathbf{U}(t)$ contained in the plane $\{u_2 = 0\}$ and such that $\mathbf{U}(t) \rightarrow E_1$ as $t \rightarrow -\infty$ and $\mathbf{U}(t) \rightarrow E_3$ as $t \rightarrow +\infty$.

Moreover, reducing to the phase plane (u_1, u_2) , the critical point $(1, 0)$ (corresponding to E_1) is instead a global attractor and the point $(0, 1)$ (corresponding to E_2) is a saddle point, so that in the three-dimensional setting, the stable manifold of E_1 is the whole plane $\{u_3 = 0\}$ and its unstable manifold is the orbit \mathcal{C}_1 .

A similar discussion (by the symmetry of the system) applies to the critical points E_2 and E_3 and we have the orbit \mathcal{C}_2 connecting E_2 to E_1 in the plane $\{u_3 = 0\}$, and \mathcal{C}_3 connecting E_3 to E_2 in the plane $\{u_1 = 0\}$ (see Fig. 9.1).

Considering now the coexistence equilibrium E^* we have

$$J(E^*) = -\frac{1}{1 + \alpha + \beta} \begin{pmatrix} 1 & \alpha & \beta \\ \beta & 1 & \alpha \\ \alpha & \beta & 1 \end{pmatrix}$$

and it is possible to compute its eigenvalues

$$\lambda_1 = -1 \quad \lambda_{2,3} = \frac{\alpha + \beta - 2 \pm i\sqrt{3}(\alpha - \beta)}{2(\alpha + \beta + 1)}.$$

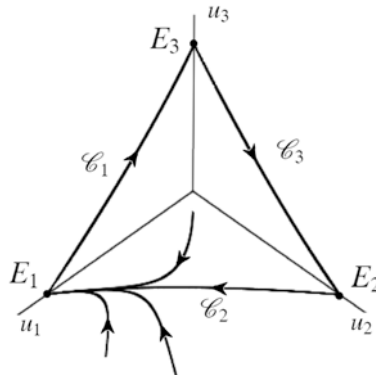


Fig. 9.1 Cyclical competition for system (9.2). Within the three-dimensional context, each equilibrium E_i is a saddle point with a coordinate plane as the stable manifold and a curve \mathcal{C}_i as the unstable one

Thus, if $\alpha + \beta < 2$ all eigenvalues have negative real part and E^* is asymptotically stable. Actually it is possible to prove (see Problem 9.1) that it is a global attractor as it is shown in Fig. 9.2-(a).

If instead

$$\alpha + \beta > 2. \quad (9.3)$$

$\lambda_{2,3}$ have positive real part, so that E^* is a saddle point. Its stable manifold is the line $\mathcal{L} \equiv \{u_1 = u_2 = u_3\}$. Indeed, if $\mathbf{U}(0) = (\bar{u}, \bar{u}, \bar{u}) \in \mathcal{L}$, then the solution of (9.2) has the form

$$\mathbf{U}(t) = (u(t), u(t), u(t))$$

where $u(t)$ is the solution of the scalar problem

$$u'(t) = (1 - (1 + \alpha + \beta)u(t))u(t), \quad u(0) = \bar{u}.$$

Thus, since

$$\lim_{t \rightarrow +\infty} u(t) = \frac{1}{1 + \alpha + \beta},$$

we have

$$\lim_{t \rightarrow +\infty} \mathbf{U}(t) = E^*.$$

Finally, the unstable manifold of E^* is a two-dimensional surface transverse to \mathcal{L} .

To understand the global behavior of the solutions in this case, we introduce the function

$$V(u_1, u_2, u_3) = \frac{u_1 u_2 u_3}{(u_1 + u_2 + u_3)^3}.$$

We obtain, using (9.3),

$$\begin{aligned} \dot{V}(u_1, u_2, u_3) &= \left(1 - \frac{\alpha + \beta}{2}\right) \times \\ &\times \frac{u_1 u_2 u_3}{(u_1 + u_2 + u_3)^4} [(u_1 - u_2)^2 + (u_2 - u_3)^2 + (u_3 - u_1)^2] \leq 0. \end{aligned}$$

Thus, by La Salle's theorem, for any $\mathbf{U}(0) \in \{u_1 > 0, u_2 > 0, u_3 > 0\}$ we have

$$\omega(\mathbf{U}(0)) \subset \{u_1 = u_2 = u_3\} \cup \{u_1 u_2 u_3 = 0\}. \quad (9.4)$$

We have already seen that $\mathcal{L} = \{u_1 = u_2 = u_3\}$ is the stable manifold of E^* so that we know the fate of any trajectory starting in \mathcal{L} . Let then $\mathbf{U}(0) \notin \mathcal{L}$ and prove that

$$\omega(\mathbf{U}(0)) \cap \mathcal{L} = \emptyset.$$

In fact, if this were not true, also the stable manifold \mathcal{L} and the point E^* would belong to the ω -limit set (since it is invariant and closed) and this is not possible because if $E^* \in \omega(\mathbf{U}(0))$ then $\omega(\mathbf{U}(0))$ would contain an orbit of the unstable manifold of E^* (see Butler-McGehee Lemma in Appendix A) and (9.4) would be contradicted. We conclude that

$$\omega(\mathbf{U}(0)) \subset \{u_1 u_2 u_3 = 0\},$$

i.e. the ω -limit set belongs to the coordinate planes.

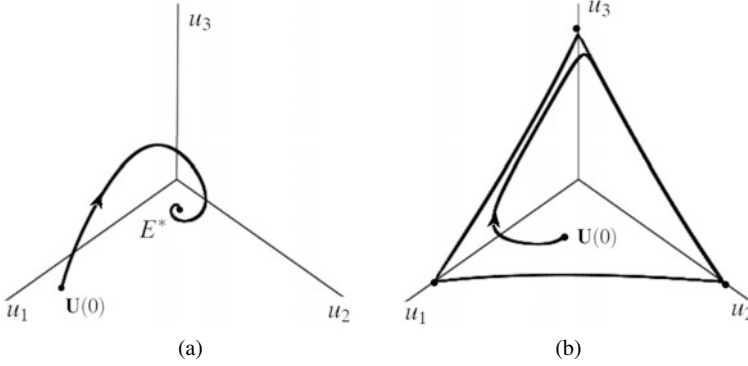


Fig. 9.2 Trajectories for system (9.2) under different conditions: (a) the case $\alpha + \beta > 2$ when E^* is a global attractor; (b) the case $\alpha + \beta < 2$ when E^* is unstable and the ω -limit set of any trajectory is $E_1 \cup \mathcal{C}_1 \cup E_2 \cup \mathcal{C}_2 \cup E_3 \cup \mathcal{C}_3$

Now, we have already analyzed the behavior of the solutions on the coordinate planes. There, the only invariant sets are the equilibria E_i and the orbits $\mathcal{C}_1, \mathcal{C}_2, \mathcal{C}_3$ that connect them, and we have to exclude E_0 because it is completely unstable. Indeed, since the equilibria are unstable, they can attract only points lying on their respective stable manifolds. In conclusion we have:

let $\alpha + \beta > 2$ and $U(0) \notin \mathcal{L}$, then

$$\omega(U(0)) = E_1 \cup \mathcal{C}_1 \cup E_2 \cup \mathcal{C}_2 \cup E_3 \cup \mathcal{C}_3.$$

From the ecological viewpoint, we observe a kind of cyclical coexistence of the three species. For some time, species 1 is dominant and the other two have very low abundances, then species 2 becomes dominant and after some more time species 3 prevails before leaving the scene to species 1 again starting a new cycle. In Fig. 9.2-(b) we show the trajectory in the phase space and in Fig. 9.3 the behavior of the three species over time. Note that the time elapsing between two substitutions tends to be larger and larger, corresponding to the fact that it takes an infinite time to go through the singular cycle

$$\mathcal{C} = \bigcup_{i=1}^3 E_i \cup \mathcal{C}_i.$$

Note also that each species reaches very low minima and these minima decrease, in fact

$$\liminf_{t \rightarrow \infty} u_i(t) = 0.$$

These results lead to conclude that, in the real world, for a system governed by such an interaction, a small stochastic perturbation would first produce extinction of one

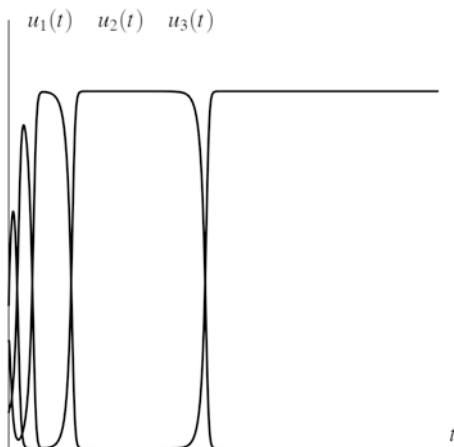


Fig. 9.3 The solutions of system (9.2) plotted versus time: each component oscillates and one component at a time is dominant

species, reducing the system to a two-dimensional one, leading to exclusion and consequently to survival of only one of the three.

Thus, although we started by defining the model as an example of cyclical coexistence, it is not considered to yield robust coexistence. Robust coexistence is rather defined through *persistence*. While the concept can be extended to much more general settings and have different meanings (see [13] for a precise and readable account of the theory), we stick here to a simple definition:

a system

$$\mathbf{Y}'(t) = \mathbf{F}(\mathbf{Y}(t)) \quad \text{with} \quad F_i(\mathbf{Y}) = y_i f_i(\mathbf{Y}) \quad (9.5)$$

and f_i defined and regular on the non-negative orthant, is persistent if there exists $\varepsilon > 0$ such that

$$\text{if } \mathbf{Y}_0 \text{ satisfies } \min_{i=1 \dots n} (Y_0)_i > 0, \quad \text{then} \quad \liminf_{t \rightarrow \infty} y_i(t) \geq \varepsilon$$

where $\mathbf{Y}(t) = (y_1(t), \dots, y_n(t))$ is the solution of (9.5) with $\mathbf{Y}(0) = \mathbf{Y}_0$.

Note that this definition corresponds to what is named *uniform strong persistence* in [13]. As seen above, system (9.2) is not persistent, according to this definition.

9.2 Two predators feeding on the same prey

We consider here the equations for two predator species competing for one prey species. We keep the the standard assumptions of Rozenzweig-MacArthur model, i.e., in the absence of predators, the prey grows logistically and, for each predator,

the functional and numerical responses are of type Holling II. Hence, the equations of the system are

$$\begin{cases} H'(t) = r \left(1 - \frac{H(t)}{K} \right) H(t) - \frac{a_1 H(t) P_1(t)}{1 + a_1 \tau_1 H(t)} - \frac{a_2 H(t) P_2(t)}{1 + a_2 \tau_2 H(t)} \\ P_1'(t) = \frac{\gamma_1 a_1 H(t) P_1(t)}{1 + a_1 \tau_1 H(t)} - \mu_1 P_1(t) \\ P_2'(t) = \frac{\gamma_2 a_2 H(t) P_2(t)}{1 + a_2 \tau_2 H(t)} - \mu_2 P_2(t) \end{cases} \quad (9.6)$$

where a_i , $i = 1, 2$ are the attack rates of the two predator species, τ_i are the handling times, γ_i are the coefficients of conversion prey-predator and μ_i are the mortality rates in the absence of preys.

First of all, we make the system non-dimensional, using the transformation

$$t \rightarrow \tilde{t} = rt, \quad H \rightarrow u = \frac{H}{K}, \quad P_i \rightarrow v_i = \frac{P_i}{\gamma_i K}.$$

This is the same scaling used in the Rozenzweig-MacArthur model, with the time scaled according to the growth rate of the prey. Then we have

$$\begin{cases} u'(t) = (1 - u(t))u(t) - \pi_1(u(t))v_1(t) - \pi_2(u(t))v_2(t) \\ v_1'(t) = (\pi_1(u(t)) - \delta_1)v_1(t) \\ v_2'(t) = (\pi_2(u(t)) - \delta_2)v_2(t) \end{cases} \quad (9.7)$$

where

$$\delta_i = \frac{\mu_i}{r}, \quad \pi_i(x) = \frac{\beta_i x}{1 + \alpha_i x}, \quad i = 1, 2,$$

with

$$\alpha_i = a_i \tau_i K, \quad \beta_i = \frac{\gamma_i a_i K}{r}, \quad i = 1, 2.$$

We note that the model belongs to the class of competition models with dynamic resources, as discussed in Sect. 7.2. In fact (9.7) is in the form (7.12), in the case of two species competing for one resource. In Sect. 7.3 we have seen that, in the case of a static resource, competition for one resource leads to exclusion of all competitor species but one. Thus we may expect that coexistence is impossible also in this case of a dynamic resource. Indeed, coexistence at equilibrium is impossible, as shown below within the analysis of steady states. However, numerical simulations show that, for certain parameter values, it is possible to find a positive periodic solution, i.e. the two predators coexist with the prey along a limit cycle (see Figs. 9.4 and 9.5).

To (partially) understand the behavior of the system and the existence of the periodic solution shown in figure, we start from the analysis of the local stability of the equilibrium points (and of some periodic solutions) of system (9.7).

First we note that, as expected, the extinction equilibrium $O \equiv (0, 0, 0)$ is unstable, as it is easy to check by the Jacobian.

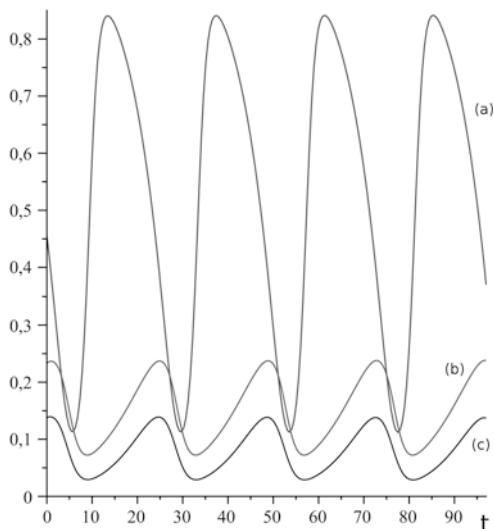


Fig. 9.4 A periodic solution of the model (9.7); curve (a) represents $u(t)$, curve (b) is $v_1(t)$ and curve (c) is $v_2(t)$. Parameter values are $\rho = 1.2$, $\beta_1 = 15.6$, $\beta_2 = 8.925$, $\alpha_1 = 13$, $\alpha_2 = 7.436$, $\delta = 0.9$

Concerning exclusion states, in order to avoid the trivial cases of a predator unable to survive (see (6.15)), we adopt the typical assumption

$$\beta_i > \alpha_i \delta_i, \quad i = 1, 2.$$

Then the equilibria are those found analyzing the reduced 1 prey-1 predator systems, in which one of the predators is absent. Indeed, in the planes $\{v_1 = 0\}$ and $\{v_2 = 0\}$ the system reduces to the Rosenzweig-MacArthur model of Sect. 6.4, thus we have the equilibria:

$$E_0 = (1, 0, 0) \quad E_1 = (u_1^*, \Psi_1(u_1^*), 0) \quad E_2 = (u_2^*, 0, \Psi_2(u_2^*)) \quad (9.8)$$

where

$$u_i^* = \frac{\delta_i}{\beta_i - \alpha_i \delta_i} \quad i = 1, 2$$

are the solutions of

$$\pi_i(u) = \delta_i, \quad i = 1, 2,$$

respectively, and

$$\Psi_i(u) = \frac{1}{\beta_i} (1 - u)(1 + \alpha_i u), \quad i = 1, 2.$$

For the equilibria E_i to exist it is necessary $u_i^* < 1$, otherwise the equilibrium $(1, 0)$ is the only non-trivial equilibrium for the reduced system, in the plane (u, v_i) , and it is (globally) asymptotically stable. We also remind that for the reduced sys-

tem, the equilibrium $(u_i^*, \Psi(u_i^*))$ is (globally) asymptotically stable if $\hat{u}_i < u_i^* < 1$, where \hat{u}_i is the point at which $\Psi(u)$ attains its maximum on $[0, 1]$.

We will consider only the case,

$$\hat{u}_1 = \frac{\alpha_1 - 1}{2\alpha_1} > 0$$

assuming $\alpha_1 > 1$. In fact, otherwise, existence of a periodic solution (asymptotically stable for the reduced system (u, v_1)) would not be possible. With this assumption, existence and stability of $(u_1^*, \Psi(u_1^*))$ occur under the condition

$$\hat{u}_1 < u_1^* < 1 \iff \delta_1(\alpha_1 + 1) < \beta_1 < \frac{\alpha_1 \delta_1 (\alpha_1 + 1)}{\alpha_1 - 1}, \quad (9.9)$$

while, in the case

$$u_1^* < \hat{u}_1 \iff \beta_1 > \frac{\alpha_1 \delta_1 (\alpha_1 + 1)}{\alpha_1 - 1}, \quad (9.10)$$

$(u_1^*, \Psi(u_1^*))$ is unstable and the reduced system with the prey and the predator 1 has a periodic orbit (of period T_1)

$$\Gamma_1 \equiv \{ (\bar{u}(t), \bar{v}_1(t)), \quad t \in [0, T_1] \}. \quad (9.11)$$

The orbit Γ_1 is asymptotically stable, and globally attractive from the positive half-plane, with the exception of the equilibrium $(u_1^*, \Psi(u_1^*))$ (see the discussion in Sect. 6.4). An example of the periodic solution is shown in Fig. 9.5.

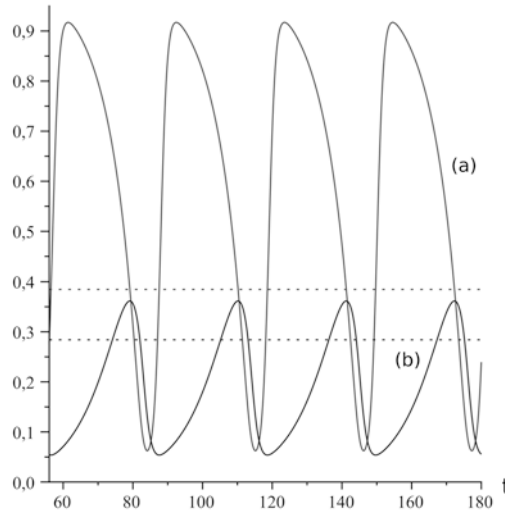


Fig. 9.5 The values of $u(t)$ (curve (a)) and $v_1(t)$ (curve (b)) over a periodic orbit of the reduced system with $v_2(t) \equiv 0$. Parameter values are $r = 1.2$, $K = 1$, $\lambda_1 = 15.6$, $d_1 = 1$, $\alpha_1 = 13$. The horizontal lines denote the values of the (unstable) equilibrium (u_1^*, v_1^*) ; it can be seen that $u(t)$ is more often above u_1^* than below, while the opposite holds for $v(t)$

Similar considerations hold for the reduced system in the phase plane (u, v_2) , when predator 1 is absent.

Finally we check existence of internal equilibrium points for the system (9.7). If $v_1 \neq 0$, the second equation in (9.7) yields $u = u_1^*$; if $v_2 \neq 0$ from the third equation we get $u = u_2^*$. Assuming, generically $u_1^* \neq u_2^*$, it turns out that there are no internal equilibria, and all the equilibria are listed in (9.8).

In what follows, let us assume, without loss of generality

$$u_1^* < u_2^*. \quad (9.12)$$

As u_i^* is the resource (i.e. the prey) level at which the population of predators i can maintain, the principle of survival of the competitor with the lowest level of necessary resource makes us think that only predator 1 will survive, while predator 2 will go extinct.

Let us now analyze the full problem, starting from the local stability of equilibria in the three-dimensional phase plane (u, v_1, v_2) . The Jacobian matrices of the system at E_i are

$$J(E_0) = \begin{pmatrix} -1 & -\pi_1(1) & -\pi_2(1) \\ 0 & \pi_1(1) - \delta_1 & 0 \\ 0 & 0 & \pi_2(1) - \delta_2 \end{pmatrix},$$

$$J(E_1) = \begin{pmatrix} \pi_1(u_1^*) \Psi'_1(u_1^*) & -\pi_1(u_1^*) & -\pi_2(u_1^*) \\ \pi'_1(u_1^*) v_1^* & 0 & 0 \\ 0 & 0 & \pi_2(u_1^*) - \delta_2 \end{pmatrix}$$

and

$$J(E_2) = \begin{pmatrix} \pi_1(u_2^*) \Psi'_2(u_2^*) & -\pi_1(u_2^*) & -\pi_2(u_2^*) \\ 0 & \pi_1(u_2^*) - \delta_1 & 0 \\ \pi'_2(u_2^*) v_2^* & 0 & 0 \end{pmatrix}.$$

Now, $J(E_0)$ is triangular; hence its eigenvalues are the elements on the diagonal: the first (-1) is certainly negative, while $\pi_1(1) - \delta_1 < 0$ if and only if $1 < u_1^*$ (actually π_1 is an increasing function and u_1^* is the solution of $\pi_1(u) = \delta_1$); similarly $\pi_2(1) - \delta_2 < 0$ if and only if $1 < u_2^*$. Thus:

E_0 is asymptotically stable if $1 < u_1^* < u_2^*$ (i.e. when the equilibria E_1 and E_2 are not feasible) and is unstable if $u_1^* < 1$.

Concerning $J(E_1)$, it is a block- triangular matrix; hence its eigenvalues are $\pi_2(u_1^*) - \delta_2$ and the eigenvalues of the top-left 2×2 matrix :

$$J_{11} = \begin{pmatrix} \pi_1(u_1^*) \Psi'_1(u_1^*) & -\pi(u_1^*) \\ \pi'_1(u_1^*) v_1^* & 0 \end{pmatrix}.$$

J_{11} is the Jacobian matrix in (u_1^*, v_1^*) of the reduced system with the prey and predator 1 only; we know that it has both eigenvalues with negative real part if and only if (9.9) is satisfied. The third eigenvalue $(\pi_2(u_1^*) - \delta_2)$ is instead always negative

under the assumption (9.12). In fact π_2 is increasing and $\pi_2(u_1^*) < \pi_2(u_2^*) = \delta_2$. In conclusion:

the equilibrium E_1 exists and is asymptotically stable, if and only if condition (9.9) holds.

Moving to the equilibrium E_2 , we can use the same arguments. However, for $J(E_2)$ one eigenvalue is $\pi_1(u_2^*) - \delta_1$ and is always positive because of (9.12), thus:

the equilibrium $J(E_2)$, if it exists, is unstable.

We now focus on the assumption (9.10) so that, for the reduced system prey-predator 1, E_1 is unstable and a periodic orbit Γ_1 (and let T_1 be its period) exists in the plane (u, v_1) and is asymptotically stable (see (9.11)). Indeed, merging Γ_1 into the phase space (u, v_1, v_2) , we have the periodic orbit

$$\tilde{\Gamma}_1 \equiv \{ (\bar{u}(t), \bar{v}_1(t), 0), \quad t \in [0, T_1] \},$$

also for the full system (9.7) and we may ask whether it is asymptotically stable also for this system. To this aim we have to linearize (9.7) at $\tilde{\Gamma}_1$ and resort to Floquet theory to determine the behavior of the linearized system through Floquet multipliers (see Appendix A).

Now, the linearized system, on the deviations from the periodic solution

$$\omega(t) = u(t) - \bar{u}(t), \quad \omega_1(t) = v_1(t) - \bar{v}_1(t), \quad \omega_2(t) = v_2(t),$$

reads

$$\begin{cases} \omega'(t) = a_{00}(t)\omega(t) + a_{01}(t)\omega_1(t) + a_{02}(t)\omega_2(t), \\ \omega'_1(t) = a_{10}(t)\omega(t) + a_{11}(t)\omega_1(t), \\ \omega'_2(t) = a_{22}(t)\omega_2(t), \end{cases} \quad (9.13)$$

where the coefficients $a_{ij}(t)$ are all periodic with period T_1 and in particular

$$a_{22}(t) = \pi_2(\bar{u}(t)) - \delta_2.$$

Then we are left with the determination of the Floquet multipliers and a first step in this direction can be performed looking at the third equation in (9.13). In fact, this equation can be solved explicitly

$$\omega_2(t) = \omega_2(0) \exp \left\{ \int_0^t (\pi_2(\bar{u}(s)) - \delta_2) ds \right\}$$

and the asymptotic behavior of $\omega_2(t)$ is the same as that of e^{zt} with

$$z = \frac{1}{T_1} \int_0^{T_1} (\pi_2(\bar{u}(s)) - \delta_2) ds. \quad (9.14)$$

In other words, one Floquet multiplier is $\lambda_3 = e^{zT_1}$.

Now, if $z > 0$, $\tilde{\Gamma}_1$ is then unstable. On the other hand, if $z < 0$, one has to look at the other Floquet multiplier λ_2 (beyond $\lambda_1 = 1$). This can be found by looking at the first two equations. Without performing any computation, one can note that these will be the same equations that would be obtained by looking at the stability of Γ_1 for the 2-dimensional system with only the prey and predator 1. We already know that, because of (9.10), Γ_1 is stable for the 2-dimensional system, hence, $|\lambda_2| < 1$. Summarizing, we have:

let z be defined in (9.14), then the periodic orbit $\tilde{\Gamma}_1$ is asymptotically stable for system (9.6) if $z < 0$ and is unstable if $z > 0$.

One may wonder whether it is possible that $z > 0$ under the assumption (9.12). In fact, $\bar{u}(s)$ will fluctuate around u_1^* and, if one substitutes u_1^* to $\bar{u}(t)$ in (9.14), one would obtain

$$\tilde{z} = \frac{1}{T_1} \int_0^{T_1} (\pi_2(u_1^*) - \delta_2) ds. = (\pi_2(u_1^*) - \delta_2) < (\pi_2(u_2^*) - \delta_2) = 0 \quad (9.15)$$

by the definition of u_2^* .

The fact is, however, that $\bar{u}(t)$, while fluctuating around u_1^* , may be more often above it than below it (see an illustration in Fig. 9.5) so that the value of z may be higher than \tilde{z} .

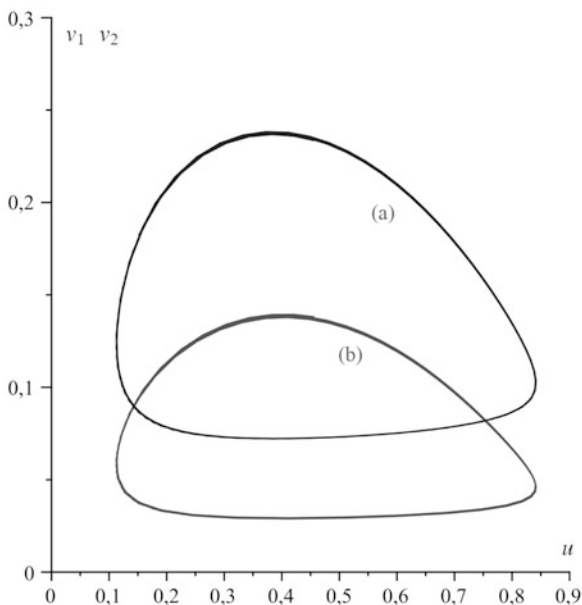


Fig. 9.6 The periodic solution of the model (9.7) of Fig. 9.5 in the phase planes (u, v_i) . Curve (a) represents (u, v_1) , curve (b) represents (u, v_2)

To make this argument precise, and find conditions allowing for $z > 0$, we first note, that by the third equation in (9.7) we have

$$\frac{1}{T_1} \int_0^{T_1} \pi_1(\bar{u}(s)) ds = \delta_1 + \frac{1}{T_1} \ln \left(\frac{\bar{v}_1(T_1)}{\bar{v}_1(0)} \right) = \delta_1.$$

Then we define the function

$$G(x) = \pi_2(\pi_1^{-1}(x)) = \frac{\beta_2 x}{\beta_1 + x(\alpha_2 - \alpha_1)}$$

such that $\pi_2(x) = G(\pi_1(x))$; it satisfies

$$G''(x) = \frac{\beta_2(\alpha_1 - \alpha_2)}{(\beta_1 + x(\alpha_2 - \alpha_1))^3}.$$

Then $G(x)$ is a convex function if $\alpha_1 > \alpha_2$ and by Jensen's inequality we have

$$\begin{aligned} \frac{1}{T_1} \int_0^{T_1} \pi_2(\bar{u}(s)) ds &= \frac{1}{T_1} \int_0^{T_1} G(\pi_1(\bar{u}(s))) ds \\ &> G\left(\frac{1}{T_1} \int_0^{T_1} \pi_1(\bar{u}(s)) ds\right) = G(1) = G(\pi_1(u_1^*)) = \pi_2(u_1^*). \end{aligned}$$

Since $\pi_2(u_1^*) < \pi_2(u_2^*) = \delta_2$ the inequality $z > 0$ is not in contradiction with the previous inequality and the numerical example in Figs. 9.5 and 9.6 shows that indeed this is possible.

On the other hand, if $\alpha_1 \leq \alpha_2$, Jensen's inequality in the opposite direction shows that $z < 0$. Hence, having chosen (9.12), (9.10) and $\alpha_1 > \alpha_2$ are necessary conditions for the instability of all boundary attractors. This still does not guarantee that $z > 0$, but, with a careful search, one can find parameter values (for instance those used in Figs. 9.5 and 9.6) yielding $z > 0$. General theory of dynamical systems then implies that, when all boundary attractors are unstable, an internal attractor exists, in this case a periodic solution.

Although numerical evidence shows that, with these parameter values, almost all initial values are attracted to the periodic solution which stays at a positive distance from the coordinate axes, system (9.7) is not persistent. In fact, the equilibrium E_1 is a saddle point with its stable manifold pointing towards the interior of the positive orthant. Thus, there exist initial values with all coordinates positive that are attracted to E_1 , so that $\lim_{t \rightarrow \infty} v_2(t) = 0$, in contrast to the definition of persistence.

9.3 The food chain model

In this section, we consider another 3-species system, namely a food chain composed by a first species (the bottom of the chain) that in the absence of other species undergoes logistic growth, a first specialist predator (predator 1) feeding on the previous species and a second specialist predator (predator 2, the top of the chain) feeding on predator 1. Denoting by $H(t)$, $P_1(t)$, $P_2(t)$ the respective abundances we have the

model

$$\begin{cases} H'(t) = rH(t) \left(1 - \frac{H(t)}{K}\right) - \frac{a_1 H(t) P_1(t)}{1 + a_1 T_1 H(t)} \\ P_1'(t) = \frac{\gamma_1 a_1 H(t) P_1(t)}{1 + a_1 T_1 H(t)} - \mu_1 P_1(t) - \frac{a_2 P_1(t) P_2(t)}{1 + a_2 T_2 P_1(t)} \\ P_2'(t) = \frac{\gamma_2 a_2 P_1(t) P_2(t)}{1 + a_2 T_2 P_1(t)} - \mu_2 P_2(t) \end{cases} \quad (9.16)$$

where we adopt functional responses of Holling II type. This system has been studied by several authors [5, 7, 9] and turned out to be rather difficult to analyze, and to display several different dynamical behaviors, according to parameter values. Here we limit ourselves to the more basic steps, referring to the literature for detailed bifurcation analysis. A different version of this model, describing the food chain using Lotka-Volterra interactions, is instead easier to analyze, and yields a much simpler dynamical behavior (see Problem 9.2).

A convenient scaling of the system is obtained through the transformation

$$t \rightarrow \tilde{t} = rt, \quad H \rightarrow u = \frac{H}{K}, \quad P_1 \rightarrow v = \frac{P_1}{\gamma_1 K}, \quad P_2 \rightarrow w = \frac{P_2}{\gamma_1 \gamma_2 K},$$

by which we obtain the dimensionless system

$$\begin{cases} u'(t) = u(t)(1 - u(t)) - \pi_1(u(t))v(t) \\ v'(t) = \pi_1(u(t))v(t) - \delta_1 v(t) - \pi_2(v(t))w(t) \\ w'(t) = (\pi_2(v(t)) - \delta_2)w(t), \end{cases} \quad (9.17)$$

where we have

$$\delta_1 = \frac{\mu_1}{r}, \quad \delta_2 = \frac{\mu_2}{r}$$

and

$$\pi_i(x) = \frac{\beta_i x}{1 + \alpha_i x} \quad i = 1, 2,$$

with

$$\alpha_1 = a_1 T_1 K, \quad \alpha_2 = \gamma_1 a_2 T_2 K, \quad \beta_1 = \frac{\gamma_1 a_1 K}{r}, \quad \beta_2 = \frac{\gamma_1 \gamma_2 a_2 K}{r}.$$

Then we focus on the dynamics of the system, under the assumptions

$$\beta_1 > \delta_1 \alpha_1, \quad \beta_2 > \delta_2 \alpha_2$$

that are necessary to avoid the trivial cases of predators unable to survive at any density of their preys.

Concerning equilibria, we have as usual the extinction state $O \equiv (0, 0, 0)$ which is a saddle point. The u -axis, corresponding to the case of the bottom species living in the absence of the predators, is its unstable manifold connecting it to the equilibrium $E_1 \equiv (1, 0, 0)$. This latter is unstable if

$$\pi_1(1) - \delta_1 > 0$$

and its unstable manifold lies in the (u, v) -plane.

The reduced system in the phase plane (u, v) , corresponding to the absence of the top predator, is a Rosenzweig-MacArthur model and, as discussed in Sect. 6.4, there exists a coexistence equilibrium (u_0^*, v_0^*) determined by

$$\pi_1(u_0^*) - \delta_1 = 0 \quad \text{and} \quad v_0^* = \Psi_1(u_0^*),$$

where

$$\Psi_1(x) = \frac{1}{\beta_1}(1-x)(1+\alpha_1x).$$

The equilibrium is feasible if

$$u_0^* < 1 \iff \beta_1 > \delta_1(1+\alpha_1). \quad (9.18)$$

Moreover such a point is asymptotically stable and a global attractor in the phase plane (u, v) if

$$u_0^* > \hat{u} = \frac{\alpha_1 - 1}{2\alpha_1} \iff \beta_1(\alpha_1 - 1) < \delta_1\alpha_1(\alpha_1 + 1),$$

while it is unstable if

$$u_0^* < \hat{u}.$$

Thus, in the three-dimensional setting, if (9.18) is satisfied, we have the equilibrium

$$E_0^* \equiv (u_0^*, v_0^*, 0).$$

Note that the condition $u_0^* < 1$ for the feasibility of E_0^* can be written as

$$\pi_1(1) - \delta_1 > \pi_1(u_0^*) - \delta_1 = 0$$

so that E_0^* exists if and only if the equilibrium E_1 is unstable.

For the existence of a coexistence point $E^* \equiv (u^*, v^*, w^*)$ we have to solve the system

$$\begin{cases} v = \Psi_1(u) \\ \pi_1(u)v - \delta_1v - \pi_2(v)w = 0 \\ \pi_2(v) = \delta_2 \end{cases} \quad (9.19)$$

and we can proceed as follows. First we solve the third equation and find

$$v^* = \frac{\delta_2}{\beta_2 - \alpha_2\delta_2} > 0. \quad (9.20)$$

Then we consider the first

$$\Psi_1(u) = v^* \quad (9.21)$$

and look for real solutions u^* . Finally, from the second equation, for each u^* we find

$$w^* = \frac{(\pi_1(u^*) - \delta)v^*}{\pi_2(v^*)} = \frac{(\pi_1(u^*) - \delta)v^*}{\delta_2}.$$

Note that the above computation is successful and the equilibrium E^* feasible, if and only if (9.21) has a real solution satisfying

$$u^* > u_0^*. \quad (9.22)$$

In fact, only in this case we have

$$w^* = (\pi_1(u^*) - \delta_1)v^* > (\pi_1(u_0^*) - \delta_1)v^* = 0.$$

As the solutions of (9.21) necessarily satisfy $u^* < 1$, since $\Psi_1(x) \leq 0$ for $x \geq 1$, a necessary condition for the feasibility of E^* is $u_0^* < 1$, i.e. (9.18), which will then be always assumed in what follows.

In order to discuss the existence of E^* it is convenient to choose δ_2 as a parameter to vary and look for feasibility of E^* . Actually, Equation (9.21) can be solved explicitly and the feasibility of E^* can be easily discussed algebraically. However, we can provide a clear graphical discussion looking for intersections of a fixed parabola $y = \Psi(u)$ with the horizontal line $y = v^*$ that, instead, increases with δ_2 , according to relation (9.20).

Under the basic assumptions we have two possible scenarios we discuss separately.

Case 1. $\hat{u} < u_0^*$

This case is illustrated in Fig. 9.7, assuming $\hat{u} > 0$, i.e. $\alpha_1 > 1$; no essential differences occur when $\hat{u} < 0$ (i.e. $\alpha_1 < 1$).

From Fig. 9.7 we see that eq. (9.21) has only one acceptable solution if and only if the condition

$$\tilde{\Psi}_1(u_0^*) > v^* \iff \frac{\delta_2}{\beta_2 - \alpha_2 \delta_2} < \Psi_1(u_0^*) \iff \delta_2 < \delta_2^* = \frac{\beta_2 \Psi_1(u_0^*)}{1 + \alpha_2 \Psi_1(u_0^*)} \quad (9.23)$$

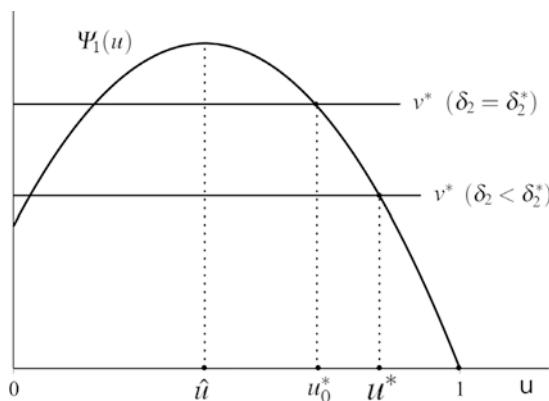


Fig. 9.7 Existence of a coexistence equilibrium E^* in the case $\hat{u} < u_0^*$. Only one acceptable intersection between the parabola and the horizontal line $y = v^*$ occurs; this happens when δ_2 is small enough that the intersection occurs at $u^* > u_0^*$. Bifurcation occurs at $\delta_2 = \delta_2^*$ when the horizontal line intersects the parabola at u_0^* . The corresponding bifurcation graph, is reported in Fig. 9.9 together with stability analysis

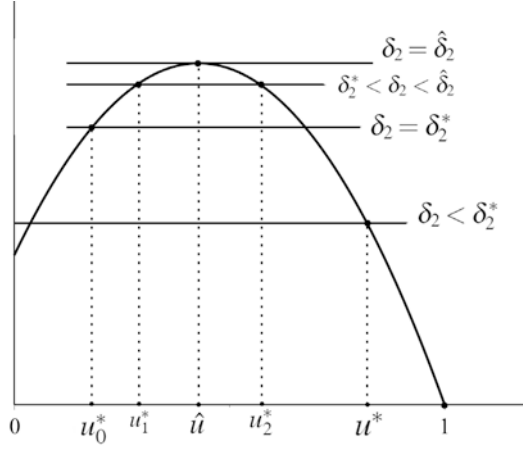


Fig. 9.8 Existence of a coexistence equilibrium E^* in the case $\hat{u} > u_0^*$. Here a first bifurcation point occurs at $\delta_2 = \hat{\delta}_2$ when the horizontal line $y = v^*$ is tangent to the parabola $\Psi(u)$ at its vertex. At this point, two solutions arise, both on the right of u_0^* ($\delta_2^* < \delta_2 < \hat{\delta}_2$). One of these solution is lost at $\delta_2 = \delta_2^*$ when the horizontal line crosses the parabola at u_0^* and, for $\delta_2 < \delta_2^*$, only one solution is on the right of u_0^* . The corresponding bifurcation graph and stability analysis is shown in Fig. 9.10

is satisfied. Thus, concerning existence of equilibria, we have the bifurcation graph shown in Fig. 9.9.

Case 2. $\hat{u} > u_0^*$

This case, illustrated in Fig. 9.8, allows for the existence of multiple equilibria. In fact, there are three possibilities, according to the height of the horizontal line $y = v^*$, with switching points $\delta_2 = \delta_2^*$ (see (9.23)) and $\delta_2 = \hat{\delta}_2$, where

$$\frac{\hat{\delta}_2}{\beta_2 - \alpha_2 \hat{\delta}_2} = \Psi_1(\hat{u}) \iff \hat{\delta}_2 = \frac{\beta_2 \Psi_1(\hat{u})}{1 + \alpha_2 \Psi_1(\hat{u})}.$$

Namely we have:

- if $\Psi_1(\hat{u}) < v^*$ ($\delta_2 > \hat{\delta}_2$)
then (9.21) has no real solutions;
- if $\Psi_1(u_0^*) < v^* < \Psi_1(\hat{u})$ ($\delta_2^* < \delta_2 < \hat{\delta}_2$)
then (9.21) has two solutions u_1^* and u_2^* , both satisfying $u_i^* > u_0^*$; hence there are two coexistence equilibria;
- if $\Psi_1(u_0^*) > v^*$ ($\delta_2 < \delta_2^*$)
then (9.21) has only one solution u^* satisfying $u^* > u_0^*$; hence there exists a unique coexistence equilibrium.

In this case, we have the bifurcation graph shown in Fig. 9.10, where also stability switches are indicated.

Let us now study the stability of the equilibria. At E_0^* the Jacobian is

$$J(E_0^*) = \begin{pmatrix} \delta \Psi_1'(u_0^*) & -\delta_1 & 0 \\ \pi_1'(u_0^*) & 0 & -\pi_2(v_0^*) \\ 0 & 0 & \pi_2(v_0^*) - \delta_2 \end{pmatrix}, \quad (9.24)$$

and one eigenvalue is

$$\lambda_3 = \pi_2(v_0^*) - \delta_2,$$

while the two others are those of the upright-left 2×2 matrix which is the Jacobian of the reduced system at (u_0^*, v_0^*) .

In case 1, (u_0^*, v_0^*) is asymptotically stable for the reduced system. Thus, E_0^* is asymptotically stable when $\lambda_3 < 0$, i.e. for

$$\pi_2(v^*) = \delta_2 > \pi_2(v_0^*) \iff v_0^* < v^*$$

and is unstable if $v_0^* > v^*$. Remembering that $v_0^* = \Psi_1(u_0^*)$, the inequality $v_0^* > v^*$ is exactly condition (9.23), thus instability of E_0^* occurs for $\delta_2 < \delta_2^*$. The equilibrium E^* arising at $\delta_2 = \delta_2^*$ inherits the stability of E_0^* for δ_2 close to (and smaller than) δ_2^* .

In case 2, (u_0^*, v_0^*) is unstable for the reduced system. Thus, E_0^* is always unstable.

An extensive analysis of the (2 parameter) bifurcation diagram for this system is presented in [7]. Here we limit ourselves at a partial analysis of the stability of E^* and a short description of overall patterns.

We compute the Jacobian J^* at the equilibrium E^* , by first performing some simplifications. Indeed for some entries we have

$$(J^*)_{33} = \pi_2(v^*) - \delta_2 = 0,$$

because of the third of (9.19), and

$$(J^*)_{22} = \pi_1(u^*) - \delta_1 - \pi_2'(v^*)w^* = (\pi_1(u^*) - \delta_1) \left(1 - \frac{v^* \pi_2'(v^*)}{\pi_2(v^*)} \right)$$

because of the second of (9.19). Computing explicitly $\pi_2(v)$ and $\pi_2'(v)$, we obtain

$$(J^*)_{22} = (\pi_1(u^*) - \delta_1) \frac{1}{1 + \alpha_2 v^*} > 0.$$

Writing the first of (9.17) as

$$u'(t) = \pi_1(u(t)) (\Psi_1(u(t)) - v(t))$$

we obtain

$$(J^*)_{11} = \pi_1(u^*) \Psi_1'(u^*).$$

Thus we finally have

$$J^* = \begin{pmatrix} \pi_1(u^*)\Psi'_1(u^*) & -\pi_1(u^*) & 0 \\ \pi'_1(u^*)u^* & (J^*)_{22} & -\pi_2(v^*) \\ 0 & \pi'_2(v^*)v^* & 0 \end{pmatrix}. \quad (9.25)$$

Now, in order to use Routh-Hurwitz conditions to state if E^* is asymptotically stable, we compute the coefficients

$$a_1 = -\text{tr}(J^*) = L_1 - L_2$$

$$a_2 = \begin{vmatrix} \pi_1(u^*)\Psi'_1(u^*) & -\pi_1(u^*) \\ \pi'_1(u^*)u^* & (J^*)_{22} \end{vmatrix} + \begin{vmatrix} (J^*)_{22} & -\pi_2(v^*) \\ \pi'_2(v^*)v^* & 0 \end{vmatrix} = -L_1L_2 + p_1 + p_2$$

$$a_3 = -\det(J^*) = L_1p_2$$

where, to simplify notation, we have used the following definitions:

$$p_1 = \pi_1(u^*)\pi'_1(u^*)u^*, \quad p_2 = \pi_2(v^*)\pi'_2(v^*)v^*,$$

$$L_1 = -\pi_1(u^*)\Psi'_1(u^*), \quad L_2 = (J^*)_{22}.$$

Then, for E^* to be asymptotically stable, we check if a_1 , a_2 , a_3 , $a_1a_2 - a_3$ are all positive.

Note that p_1 , p_2 and L_2 are always positive; L_1 is positive (hence $a_3 > 0$) if $u^* > \hat{u}$, thus always in case 1, and for the larger of the two (or the unique, when only one) solutions in case 2, while L_1 is negative (hence $a_3 < 0$) for the smaller solution in case 2 (when $\delta_2^* < \delta_2 < \hat{\delta}_2$).

To obtain some information on the stability of E^* , again we study, separately for cases 1 and 2, how a_1 , a_2 and $a_1a_2 - a_3$ (there is no need to study a_3 as seen above) vary as δ_2 decreases. Notice that these depend on δ_2 as p_1 , L_1 and L_2 depend on u^* , which depends on δ_2 .

In case 1, E^* exists for $\delta_2 > \delta_2^*$, bifurcating from E_0^* ; thus

$$\lim_{\delta_2 \rightarrow \delta_2^{*-}} u^* = u_0^*, \quad \text{and} \quad \lim_{\delta_2 \rightarrow \delta_2^{*-}} v^* = v_0^*.$$

This means that, for $\delta_2 \rightarrow \delta_2^{*-}$, L_2 approaches 0, while all other quantities tend to a positive value. Thus, for δ_2 close to and smaller than δ_2^* , a_1 , a_2 and a_3 are positive, while $a_1a_2 - a_3 \approx \rho L_1 p_1 > 0$. Hence, E^* is asymptotically stable for δ_2 close to δ_2^* , as expected because of the exchange of stability in transcritical bifurcations.

When δ_2 goes to 0, v^* converges to 0 because of (9.20), so that u^* converges to 1 (see Fig. 9.7); computing the values of p_1 , p_2 , L_1 and L_2 for $u^* = 1$, $v^* = 0$, we see that

$$p_1 \rightarrow \frac{\beta_1^2}{(1 + \alpha_1)^3} \quad p_2 \rightarrow 0, \quad L_1 \rightarrow 1 \quad L_2 \rightarrow \frac{\beta_1}{1 + \alpha_1} - \delta_1$$

as δ_2 goes to 0. Hence, for δ_2 close to 0,

$$a_1 \approx 1 + \delta_1 - \frac{\beta_1}{1 + \alpha_1}, \quad a_2 \approx \frac{\beta_1^2}{(1 + \alpha_1)^3} + \delta_1 - \frac{\beta_1}{1 + \alpha_1} \text{ and } a_3 \approx 0.$$

Then E^* will be asymptotically stable, for δ_2 close to 0, if and only if both a_1 and a_2 are positive, corresponding respectively to

$$\delta_1 > \frac{\beta_1}{1 + \alpha_1} - 1 \quad (9.26)$$

and

$$\delta_1 > \frac{\beta_1}{1 + \alpha_1} \left(1 - \frac{\beta_1}{(1 + \alpha_1)^2} \right). \quad (9.27)$$

If either of the two inequalities is reversed, then the equilibrium E^* will be unstable for δ_2 close to 0.

Thus, for δ_1 large enough, E^* is asymptotically stable both for δ_2 close to δ_2^* and for δ_2 close to 0. Numerical evidence suggests that in this case, E^* is asymptotically stable for all values of $\delta_2 < \delta_2^*$.

Instead, if δ_1 is small enough that either (9.26) or (9.27) is reversed, necessarily there exists a value $\delta_2^\#$ at which $a_1 a_2 - a_3 = 0$, while $a_1 a_2 - a_3 > 0$ for $\delta_2 > \delta_2^\#$; hence a Hopf bifurcation occurs at $\delta_2^\#$. Again, the numerical analysis by [7] shows (at

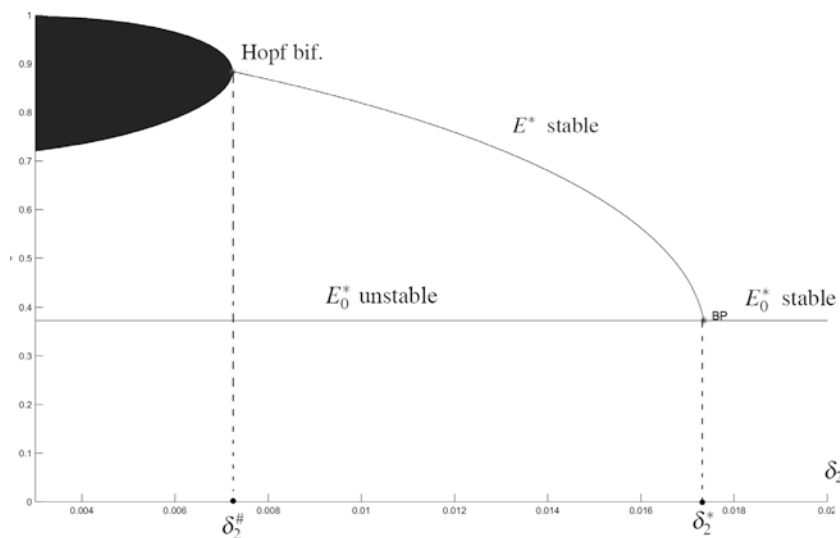


Fig. 9.9 Bifurcation picture for case 1. The coexistence equilibrium E^* bifurcate from E_0^* at $\delta_2 = \delta_2^*$ inheriting its stability for $\delta_2 < \delta_2^*$. If δ_1 is such that (9.26) and (9.27) hold, then E^* is a global attractor for any $\delta_2 < \delta_2^*$. If either of the inequalities (9.26) and (9.27) is reversed (the case shown in the picture), then there exists a value $\delta_2^\#$ such that for $\delta_2^\# < \delta_2 < \delta_2^*$ all solutions converge to the coexistence equilibrium E^* while, for $\delta_2 < \delta_2^\#$, all solutions converge to a periodic solution with all species present

least for the parameter region studied) that no other equilibrium bifurcations occur, that the bifurcation at $\delta_2^\#$ is supercritical, so that a branch of stable periodic solutions arises for $\delta_2 < \delta_2^\#$, and that no bifurcations occur at this branch of periodic solutions. Then, partly relying on numerical evidence, we can conclude that:

in case 1, for $\delta_2 > \delta_2^*$ all solutions converge to the prey-predator equilibrium E_0^* ; if δ_1 is such that (9.26) and (9.27) hold, then for $\delta_2 < \delta_2^*$ all solutions converge to the coexistence equilibrium E^* ; otherwise, there exists a value $\delta_2^\#$ such that for $\delta_2^\# < \delta_2 < \delta_2^*$ all solutions converge to the coexistence equilibrium E^* ; for $\delta_2 < \delta_2^\#$, all solutions converge to a periodic solution with all species present.

Let us now look at case 2. Coexistence equilibria on the lower branch are certainly unstable as $L_1 < 0$, so that $a_3 < 0$. As for the upper branch, as δ_2 converges to $\hat{\delta}_2$, u^*

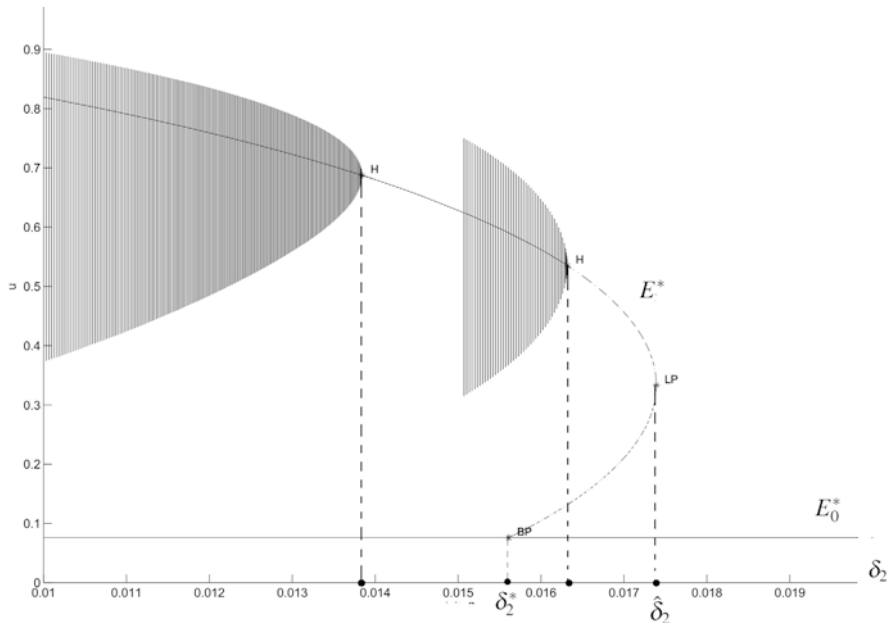


Fig. 9.10 Bifurcation graph for case 2. The lower coexistence equilibrium bifurcates from E_0^* at $\delta_2 = \delta_2^*$ (BP), and is completely unstable. At $\delta_2 = \hat{\delta}_2$ (LP), the upper coexistence equilibrium is reached through a tangent bifurcation. The two points marked (H) correspond to Hopf bifurcations; decreasing δ_2 from $\hat{\delta}_2$ on the upper branch, E^* becomes asymptotically stable at the first (H) point through a subcritical Hopf bifurcation: the initial part of the branch of (unstable) periodic solutions emerging from that point is also shown. At the second Hopf point, E^* becomes unstable through a supercritical Hopf bifurcation, giving rise to a branch of (attracting) periodic solutions, also shown on the graph. As discussed in the text, there exist several other branches of periodic solutions with a complex bifurcation structure, that are not shown

converges to \hat{u} , so that L_1 converges to 0, while L_2 converges to a positive quantity; thus $a_1 < 0$ for δ_2 close to $\hat{\delta}_2$ and E^* is unstable. Whether E^* is asymptotically stable for δ_2 close to 0 depends on the sign of (9.26) and (9.27). The numerical bifurcation diagrams computed by [7] show that, when E^* is unstable also for δ_2 close to 0, two Hopf bifurcations occur as δ_2 decreases from $\hat{\delta}_2$ to 0, so that in the region between the two Hopf bifurcations, E^* is asymptotically stable.

In case 2, we know that there exists a periodic orbit Γ_0 , image of a solution $U(t) = (\bar{u}_0(t), \bar{v}_0(t), 0)$, $t \in [0, T]$, that is attractive on the plane (u, v) . Following the same reasoning used in Sect. 9.2, it is not difficult to see that Γ_0 is asymptotically stable (resp. unstable) in the whole space according to whether

$$\frac{1}{T} \int_0^T \pi_2(\bar{v}_0(t)) dt < \delta_2 \quad (\text{resp.} \quad > \delta_2). \quad (9.28)$$

As $\bar{v}_0(t)$ does not depend on the parameter δ_2 , it is obvious that there exists a value $\delta_2^{*c} = \frac{1}{T} \int_0^T \pi_2(\bar{v}_0(t)) dt$ such that Γ_0 is asymptotically stable for $\delta_2 > \delta_2^{*c}$, unstable for $\delta_2 < \delta_2^{*c}$. At δ_2^{*c} a transcritical bifurcation of the limit cycle will occur, with a positive limit cycle arising from it.

However, the picture arising from numerical bifurcation studies is much more complex than this simple computation suggests: there are several tangent bifurcations of limit cycles, so that multiple limit cycle exist in certain parameter regions. Moreover, there are also cascades of period-doubling bifurcations of periodic solutions, which is one of main routes to chaos, as seen in the numerical study of the discrete logistic equation. We refer to [7] for more information on this point. An example of chaotic solutions is provided in Fig. 9.11.

The presence of chaotic solutions in this system is generally interpreted as arising from the coupling of two systems (H - P_1 , the predator-prey, and P_1 - P_2 , predator-top predator) that have the tendency to oscillate with independent frequencies. Indeed, as we have seen, chaos does not arise when the predator-prey system has no sustained

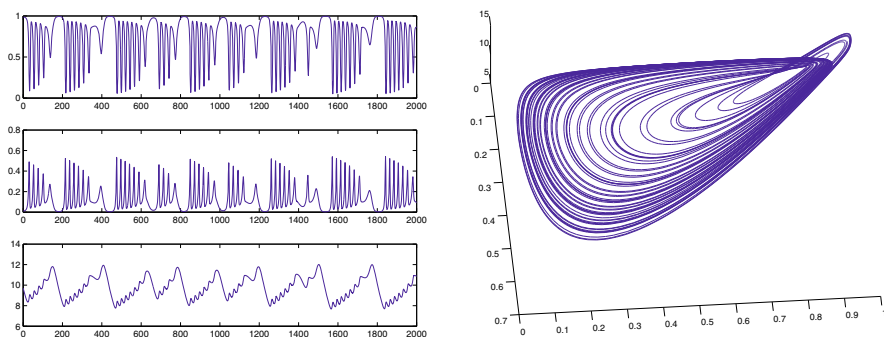


Fig. 9.11 A solution of system 9.17 in a parameter region yielding chaotic solutions. Parameter values are $\beta_1 = 5$, $\beta_2 = 0.1$, $\alpha_1 = 3$, $\alpha_2 = 2$, $\delta_1 = 0.3$, $\delta_2 = 0.009$; initial values $u_0 = 0.9862$, $v_0 = 0.0113$, $w_0 = 9.7248$. In the left panel, the three coordinates u , v and w as functions of t . In the right panel, a 3-dimensional view of the solution in the phase space (u, v, w)

oscillations (case 1, $u_0^* > \hat{u}$). On the other hand, when the predator-prey system tends to oscillate (case 2, $u_0^* > \hat{u}$), one may have positive periodic solutions on frequencies close to that of the H - P_1 system, or of the P_1 - P_2 system; or else the two frequencies may interact, leading sometimes to an asymptotically stable positive equilibrium, in other cases to resonances or chaos.

This can be seen quite clearly in Fig. 9.11, where fast oscillation of the u - v pair (with minor influences on w) coexist with a slower trend of slow increases followed by sharp decreases of w . Although at first sight the solution may almost look periodic, irregularities can clearly be seen. However, such solutions allow for a degree of predictability, not only short-term, but also from peak to peak, as has been aptly named by Rinaldi and co-authors in [2].

As we have seen, the dynamics of this system is rather complex, and difficult to establish without extensive numerical computations. On the other hand, it is not too difficult proving persistence results [13, Section 8.4]. Precisely, they show that if

$$\delta_2 < \delta_2^* \text{ and (in case 2) } \delta_2 < \frac{1}{T} \int_0^T \pi_2(\bar{v}_0(t)) dt < \delta_2 \text{ (recall (9.28))}$$

the system is persistent, i.e. there exists $\varepsilon > 0$ such that

$$\forall u(0), v_1(0), v_2(0) > 0, \quad \liminf_{t \rightarrow \infty} u(t) > \varepsilon, \quad \liminf_{t \rightarrow \infty} v_1(t) > \varepsilon, \quad \liminf_{t \rightarrow \infty} v_2(t) > \varepsilon.$$

9.4 One Predator feeding on two Preys

Assume that there are two species competing according to Lotka-Volterra model of Sect. 7.9, and both of them are preyed on by another species, with a linear functional response as in Sect. 6.2. One then arrives at the system

$$\begin{aligned} H_1' &= r_1 H_1 \left(1 - \frac{H_1}{K_1} - \alpha_{12} \frac{H_2}{K_1}\right) - c_1 H_1 P, \\ H_2' &= r_2 H_2 \left(1 - \alpha_{21} \frac{H_1}{K_2} - \frac{H_2}{K_2}\right) - c_2 H_2 P, \\ P' &= \gamma_1 c_1 H_1 P + \gamma_2 c_2 H_2 P - dP \end{aligned} \tag{9.29}$$

where $H_1(t)$ and $H_2(t)$ represent the densities of the two prey species, while $P(t)$ is the predator density.

Despite its apparent simplicity, this system can display several different dynamical behaviors, depending in intricate ways on parameter values. Here we limit ourselves to a partial discussion, mainly based on the notion of persistence, of some cases that lead to interesting biological insights, while referring to [6] or [14] for more complete results.

First of all, it is convenient, as always, to scale the variables of the system, although no scaling is totally satisfactory. By setting

$$u_i = H_i/K_i, \quad v = P/(\gamma_1 K_1), \quad \bar{t} = dt$$

one arrives at

$$\begin{aligned} u_1' &= \rho_1 u_1 (1 - u_1 - \alpha_{12} u_2) - \beta_1 u_1 v, \\ u_2' &= \rho_2 u_2 (1 - \alpha_{21} u_1 - u_2) - \beta_2 u_2 v, \\ v' &= v(\beta_1 u_1 + \eta \beta_2 u_2 - 1) \end{aligned} \quad (9.30)$$

where all parameters are appropriately defined from the original ones (Problem 9.4), noting that also α_{12} and α_{21} have been redefined.

On the coordinate-plane (u_1, u_2) system (9.30) reduces to the Lotka-Volterra system (7.49), while on the coordinate-planes (u_1, v) and (u_2, v) it reduces to system (6.11). Thus, we know well the dynamics of the system on the coordinate planes, in particular the equilibria of the reduced system, that correspond to equilibria of (9.30). Precisely there exist

- $E_1 = (1, 0, 0)$ and $E_2 = (0, 1, 0)$ that are stable for the reduced system if $\alpha_{21} > 1 <$ (resp. $\alpha_{12} > 1$), unstable otherwise;
- $E_{12} = (E_1^*, E_2^*, 0)$ which exists if either $\alpha_{12}, \alpha_{21} < 1$ or $\alpha_{12}, \alpha_{21} > 1$ and is stable for the reduced system in the former case, unstable in the latter;
- $E_{13} = (\frac{1}{\beta_1}, 0, \frac{\rho_1}{\beta_1} (1 - \frac{1}{\beta_1}))$ and $E_{23} = (0, \frac{1}{\eta \beta_2}, \frac{\rho_2}{\beta_2} (1 - \frac{1}{\eta \beta_2}))$ that exist if $\beta_1 > 1$ (resp. $\eta \beta_2 > 1$) and are stable when they exist.

There may exist also an equilibrium $E^* = (u_1^*, u_2^*, v^*)$ with all positive coordinates. It is easy to see that its coordinates should be solutions of the linear system

$$\begin{aligned} u_1 + \alpha_{12} u_2 + \frac{\beta_1}{\rho_1} v &= 1 \\ \alpha_{21} u_1 + u_2 + \frac{\beta_2}{\rho_2} v &= 1 \\ \beta_1 u_1 + \eta \beta_2 u_2 &= 1. \end{aligned} \quad (9.31)$$

Conditions that ensure that the solution of (9.31) (generically assumed to be unique) belongs to the positive orthant are rather cumbersome and will not be written here. When they are satisfied, and the equilibrium E^* is feasible, its stability can be investigated through Routh-Hurwitz conditions (see [14]), but again without leading to clearly interpretable results.

Hutson and Vickers [6], building on earlier results, then suggested that, if one is interested in species coexistence, the correct question is not whether there exists an asymptotically stable coexistence equilibrium, but rather whether the solutions stay away from the coordinate planes (the boundary of the positive orthant). They then studied whether system (9.30) is persistent, according to the definition at the end of Sect. 9, though using other terms.

It turns out [6] that stability of an internal equilibrium is neither necessary, nor sufficient for persistence of system (9.30). Indeed, it is possible that the internal equilibrium is unstable, and all solutions are attracted to an internal periodic orbit, thus satisfying the definition of persistence. On the other hand, there may be an asymptotically stable internal equilibrium, but its basin of attraction includes only part of the positive orthant, while a boundary equilibrium attracts the solution starting from other initial values with all positive coordinates, violating the definition of persistence.

We are thus led to drop the issue of whether there exists an asymptotically stable internal equilibrium of (9.30), and ask instead whether the system is persistent. The question is completely answered in [6]; here, we limit ourselves to analyze some cases (others are in the Problems) using the concepts of persistence theory, as they have developed in the past decades (and nicely summarized in [13]).

In particular, we will use Theorem A.22 that leads to simple computations. In fact, all solutions on the boundary of the positive orthant are attracted to equilibria; furthermore, it is clear that there is no cycle connecting the equilibria, according to the definition of Sect. A.9; then, we simply have to check that all equilibria are weakly repelling, as defined in Theorem A.22.

Let us start from the case where one prey-species excludes the other one in the absence of the predator (without lack of generality, assume then $\alpha_{12} < 1 < \alpha_{21}$), and we ask whether they may coexist in its presence. This would be a case of *predator-mediated coexistence*, often discussed in ecological systems; the classical experiments by Paine [11] on the marine rocky intertidal community give a strong empirical support to this possibility, that we wish to explore theoretically.

The boundary equilibria are E_1 , E_2 and possibly E_{13} and E_{23} ; we have to check that none of this equilibria has a stable manifold intersecting the interior of the positive orthant. Clearly, we have to ask $\beta_1 > 1$ (otherwise E_1 would be asymptotically stable), so that E_{13} exists and is attractive from the (u_1, v) -plane. We then have to ask that the third eigenvalue of its Jacobian is positive, i.e. (using the coordinates of E_{13})

$$\frac{\alpha_{21}}{\beta_1} + \frac{\beta_2}{\rho_2} \frac{\rho_1}{\beta_1} \left(1 - \frac{1}{\beta_1}\right) < 1. \quad (9.32)$$

It is possible that E_{23} does not exist, meaning that the predator is not able to survive on species 2 alone. In this case, that occurs if $\eta\beta_2 < 1$, the only other equilibrium to check is E_2 : its stable manifold would be the plane (u_2, v) and the unstable manifold the u_1 -axis; thus it would be weakly repulsive, and the system persistent.

If instead E_{23} exists, it is attractive from the (u_2, v) -plane and we have to check that it is unstable. The condition for this is

$$\frac{\alpha_{12}}{\eta\beta_2} + \frac{\beta_1}{\rho_1} \frac{\rho_2}{\beta_2} \left(1 - \frac{1}{\eta\beta_2}\right) < 1. \quad (9.33)$$

We can then conclude:

assume $\alpha_{12} < 1 < \alpha_{21}$. Then system (9.30) is persistent if and only if $\beta_1 > 1$, (9.32) and either $\eta\beta_2 < 1$ or (9.33) hold. This is an instance of predator-mediated coexistence.

On the other hand, if $\eta\beta_2 > 1$ and (9.33) is reversed, the equilibrium E_{23} is asymptotically stable. In this case, prey 1 would exclude prey 2 in absence of predators, but is excluded when predators are present.

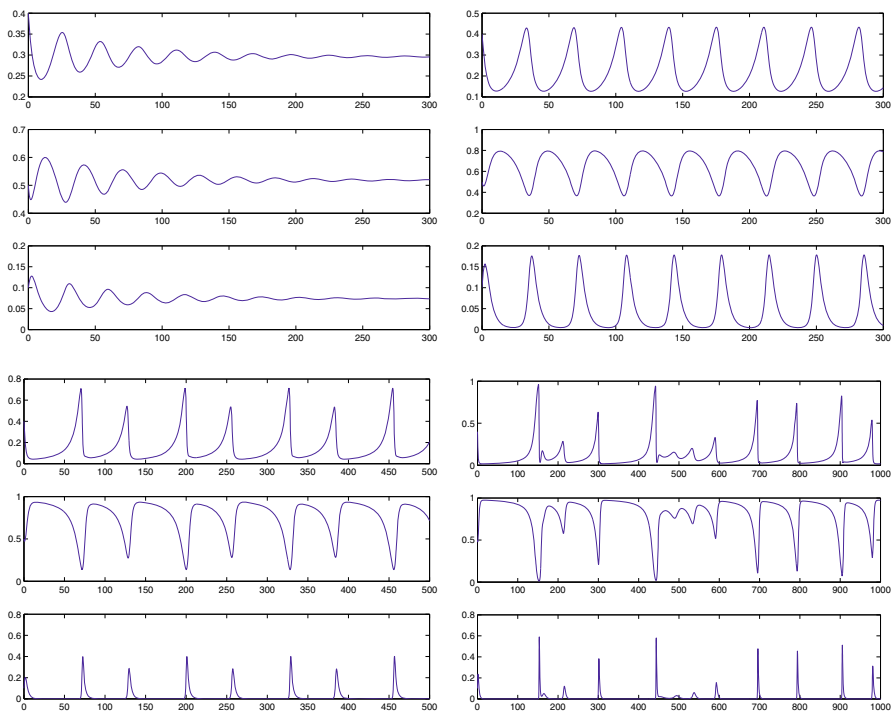


Fig. 9.12 Solutions of system (9.30). Top graph represents u_1 , middle u_2 , bottom v against time t . Common parameter values are $\alpha_{12} = 1$, $\alpha_{21} = 1.5$, $\beta_2 = 0.5$, $\rho_1 = \rho_2 = \eta_1$. Top left panel has $\beta_1 = 2.5$; top right panel $\beta_1 = 3$; bottom left $\beta_1 = 4$; bottom right $\beta_1 = 5$

Note that (9.32) and (9.33) can be interpreted as invadability conditions. We require that the density of a prey species would grow when introduced in small numbers (so that the effect of its own density on growth rate is negligible) at the equilibrium where the other prey species coexists with the predator.

Without analyzing other cases where persistence occurs or does not occur, we wish to report that, as briefly stated above, coexistence may occur not only at an asymptotically stable equilibrium, but also along a periodic solution, or a chaotic solution. The presence of chaotic solutions in system (9.30), despite its bilinear structure, had been suggested by Vance [15] and is further examined in [14]. In Figs. 9.12, we show the transition, as the parameter β_1 is increased, from an asymptotically stable coexistence equilibrium to a periodic solution through a Hopf bifurcation; and finally, through a period-doubling bifurcation, to a 2-peaked periodic solution, then, presumably through a cascade of period-doubling bifurcation, to a chaotic solution in which predator densities are generally very low, except for sudden and short bursts at slightly irregular intervals.

9.5 Chaos in Ecology

To conclude this chapter, as well as this book, we go back to the occurrence of *chaos*. In fact, as already mentioned, the discovery that so-called chaotic solutions could emerge from simple discrete-time population models exerted a strong influence on the theory of ecology, as chaos could provide a new explanation for the inherent irregularity and unpredictability of ecological systems.

The potential role of chaos in ecology has become clearer as more and more instances of chaotic solutions were shown, at least for some parameter values, in familiar models in population, like the three-species food-chain or the 2 prey-1 predator models considered in this chapter, or the epidemic SIR model with periodic contact rate. We can now say that the possibility of chaotic solutions is rather common in nonlinear systems of difference or differential equations, as long as the dimension of the system is large enough.

Together with the progress in the analysis of models, several methods have been developed to analyze data in order to assess whether they can result from a low-dimensional chaotic systems, possibly perturbed by some kind of noise. On the basis of this, several datasets (among them the cases of measles in several American and European cities in the pre-vaccine era) have been proposed as showing evidence of being the noisy output of a deterministic chaotic system, but the issue is contentious as ecological data have seldom the quality necessary for undisputed conclusions [9]. Indeed, many methods for detecting chaos from data rely on long (preferably some hundreds of data points) time series obtained under stationary conditions, something difficult to obtain in the field. This is one reason under the decision of several workers to perform instead experimental work in the laboratory.

A teamwork, led by J.M. Cushing, a mathematician, R.F. Costantino, a biologist, and B. Dennis, a statistician, has provided a large amount of data on the growth of a population of *Tribolium* [3]. After being able to fit the data with a stage-structured population model in discrete-time, of the type examined in Sect. 3.4, the authors found parameter regions of chaotic behavior. When they moved the parameters, through a careful experimental manipulation, into the chaotic region, indeed the actual population dynamics followed that pattern, thus showing that chaotic dynamics can indeed occur in populations dynamics.

A laboratory experiment not limited to a single species but involving a realistic food web has been performed by Huisman and collaborators [1]. They cultured, in a so-called microcosm, a plankton community (composed of species naturally co-occurring in the Baltic Sea) for more than 8 years under constant conditions. The results lend ample support to the occurrence of chaos in natural communities; indeed, short-term (a few days) predictability was good, but long-term (beyond 3–4 weeks) predictions were impossible. Further, the estimates of several quantities (such as Lyapunov exponents) were consistent with properties of a chaotic dynamical system.

As a provisional conclusion from the theoretical and empirical studies, we surmise that chaos should often occur in ecological systems, though it may be difficult to detect, due to the lack of sufficiently long time series and especially to the fact

that constant conditions cannot occur in the field. Thus, a degree of unpredictability is inherent in many ecological systems, however accurate would our models and measurements; furthermore, when moving from laboratory to field conditions, the effect of external noise (due to environmental factors, or the parts of the food webs that are not being modeled) should preferably be included in models.

Problems

9.1. Cyclical competition

Consider system (9.2) under the assumption $\alpha + \beta < 2$. Show that the equilibrium E^* is globally attracting. [Hint: repeat the same arguments used in the text, but noting that, when $\alpha + \beta < 2$, the sign of some inequality is reversed.]

9.2. Linear responses in the food chain model

Consider the 3-species food chain but assuming that predator functional and numerical responses are linear (it can be obtained setting $T_i = 0$ in (9.16)).

1. Show that there are 3 parameter regions where
 - a. there are no equilibria with prey coexisting with predators;
 - b. there exists a unique equilibrium E_0^* where prey and predators coexist, but no equilibrium with also the super-predators;
 - c. there exists a unique equilibrium $E^* = (u^*, v_1^*, v_2^*)$ where prey, predators and super-predators coexist.

[Here the results are presented in terms of the same scaling used to obtain (9.17).]

2. Show that in region a), the equilibrium E_1 (only prey present) is asymptotically stable; in region b), E_1 is unstable and E_0^* is asymptotically stable; in region c) E_1 and E_0^* are unstable, while E^* is asymptotically stable.
3. Using the Lyapunov function (compare to Volterra [16])

$$V(u, v_1, v_2) = (u - u^* \ln(u)) + (v_1 - v_1^* \ln(v_1)) + (v_2 - v_2^* \ln(v_2))$$

show that in region c) E^* is globally asymptotically stable.

4. With the aim of studying the influence of the prey parameters on the system, use the following scaling

$$u = \frac{H}{L}, \quad v_1 = \frac{P_1}{\gamma_1 L}, \quad v_2 = \frac{P_2}{\gamma_1 \gamma_2 L}, \quad \bar{t} = \mu_1 t, \quad \text{where } L = \frac{\mu_1}{a_1 \gamma_1}.$$

Write down the resulting system, and build a bifurcation diagram with respect to the parameter $\kappa = K/L$.

5. Discuss the relevance of this analysis towards the hypothesis that ‘the world is green’ [4] because of the presence of predators that control herbivores; better, discuss how the hypothesis could be reformulated along a gradient of productivity (see especially [10]).

6. How would the analysis of the previous two points change if system (9.16) (with $T_i > 0$) were considered?

9.3. The omnivore top predator

Extend the food-chain model of Lotka-Volterra type of previous problem, by assuming that predator 2 is an omnivore, being able to feed on the prey, as well as on the predator 1.

Write down the equations, find all equilibria with only 1 or 2 species present and study their stability. Finally, find the conditions for an equilibrium with all 3 species coexisting.

9.4. Two preys and one predator

Consider system (9.29) with 2 prey species and 1 predator.

1. Show that the scaling suggested in the text leads to (9.30), and write down the parameters of (9.30) in terms of the original parameters.
2. Find parameter values such that:
 - a. the equilibria E_1 and E_{23} are both asymptotically stable;
 - b. without predators the prey species coexist, but the introduction of the predator causes extinction of one of them [*Hint: check the stability of the boundary equilibria*];
 - c. prey species 1 would coexist with the predator, but introduction of the prey species 2 leads to extinction of both other species.

It is suggested to perform this problem with the help of a computer, so that solutions of the system can also be visualized.

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Appendix A

Basic theory of Ordinary Differential Equations

Differential Equations are somewhat pervasive in the description of natural phenomena and the theory of Ordinary Differential Equations is a basic framework where concepts, tools and results allow a systematic approach to knowledge. This same book aims to give a concrete proof of how the modeling of Nature is based on this theory and beyond. This appendix is intended to provide some concepts and results that are used in the text, referring to the student background and to textbooks for a full acquaintance of the material. We actually mention [2, 3, 5, 7, 10] as basic references on the subject.

A.1 The Cauchy problem

As a starting point of our review we recall basic results relative to the *Cauchy Problem*, under fair assumptions and conditions that allow the analysis of the models we present in the text. So we consider the following system in vector form

$$\begin{cases} \mathbf{Y}'(t) = \mathbf{F}(t, \mathbf{Y}(t)), \\ \mathbf{Y}(t_0) = \mathbf{Y}_0 \end{cases} \quad (\text{A.1})$$

where

$$\mathbf{Y}(t) \equiv (y_1(t), \dots, y_n(t)), \quad \mathbf{Y}_0 \equiv (y_1^0, \dots, y_n^0),$$

and

$$\mathbf{F}(t, \mathbf{x}) \equiv (F_1(t, x_1, \dots, x_n), \dots, F_n(t, x_1, \dots, x_n)). \quad (\text{A.2})$$

For simplicity, we assume that the function $\mathbf{F}(t, \mathbf{x})$ is defined everywhere in \mathbb{R}^{n+1} .

A first basic result on the Cauchy problem (A.1), concerns existence and uniqueness of a solution

Theorem A.1 (Existence and uniqueness). *Let the function $\mathbf{F}(t, \mathbf{x})$ be continuously differentiable in \mathbb{R}^n then, for any \mathbf{Y}_0 , there exists an interval $(t_0 - \delta, t_0 + \delta)$ and a unique continuously differentiable function $\mathbf{Y}(t)$, defined for $t \in (t_0 - \delta, t_0 + \delta)$ and satisfying (A.1).*

We will denote the solution by

$$\mathbf{Y}(t, t_0, \mathbf{Y}_0) \quad (\text{A.3})$$

where we show both the initial time t_0 and the initial datum \mathbf{Y}_0 . We note that we have the *semigroup property*

$$\mathbf{Y}(t, t_0, \mathbf{Y}_0) = \mathbf{Y}(t, t_1, \mathbf{Y}(t_1, t_0, \mathbf{Y}_0))$$

meaning that the evolution of the system depends on the initial datum, not on past history.

We see that the existence stated by Theorem A.1 is *local*, and in general the solution cannot be extended beyond a maximal finite interval. Thus (A.3) defines a function of the variables (t, t_0, \mathbf{Y}_0) on a region Ω that, in general, is strictly contained in \mathbb{R}^{n+2} , because for each t_0 and \mathbf{Y}_0 the solution is not in general globally defined. However, we have

Theorem A.2 (continuity). *Under the assumption of Theorem A.1, the function*

$$\mathbf{Y}(\cdot, \cdot, \cdot) : \Omega \rightarrow \mathbb{R}^n$$

is continuous.

In particular we have continuity with respect to the initial datum. Namely, if

$$\lim_{k \rightarrow \infty} \mathbf{Y}_k = \mathbf{Y}_\infty$$

then there exists an interval $I \equiv [t_0 - \delta, t_0 + \delta]$ such that $\mathbf{Y}(t, t_0, \mathbf{Y}_k)$ is defined in I for k sufficiently large and

$$\lim_{k \rightarrow \infty} \mathbf{Y}(t, t_0, \mathbf{Y}_k) = \mathbf{Y}(t, t_0, \mathbf{Y}_\infty), \text{ uniformly in } [t_0 - \delta, t_0 + \delta].$$

Since we deal with models requiring not only existence and uniqueness of the solution but also global existence, we need conditions ensuring that the solution is indeed defined for all $t \geq 0$. In fact we have

Theorem A.3. *Suppose that, for given t_0 and \mathbf{Y}_0 , there exists $M > 0$ such that the solution satisfies*

$$|\mathbf{Y}(t, t_0, \mathbf{Y}_0)| \leq M. \quad (\text{A.4})$$

as far as it exists, then it exists for $t \in \mathbb{R}$.

Actually boundedness of the solution is a requirement occurring in many significant results. If estimate (A.4) is satisfied only for $t \geq t_0$, then the solution is global in the future.

A second condition concerns the structure of the system.

Theorem A.4. *Suppose that there exists $M > 0$ such that*

$$\left| \frac{\partial F_i}{\partial x_i}(t, x_1, \dots, x_n) \right| \leq M.$$

Then the solution exists globally.

We are interested in describing the behavior of solutions that exists globally in time. The analysis leads to concept and results of *qualitative analysis*.

A.2 Equilibria and their stability

We focus on the autonomous case

$$\mathbf{Y}'(t) = \mathbf{F}(\mathbf{Y}(t)), \quad \mathbf{Y}(0) = \mathbf{Y}_0 \quad (\text{A.5})$$

for which the solution can be represented as $\mathbf{Y}(t, \mathbf{Y}_0)$ since any solution satisfying a condition $\mathbf{Y}(t_0) = \mathbf{Y}_0$ is then given by

$$\mathbf{Y}(t, t_0, \mathbf{Y}_0) = \mathbf{Y}(t - t_0, \mathbf{Y}_0).$$

We want to discuss the local behavior of solutions in a neighborhood of equilibria. Actually, we first identify equilibria \mathbf{Y}^* as the solutions of the equation

$$\mathbf{F}(\mathbf{Y}^*) = 0.$$

These points of the *phase space* \mathbb{R}^n correspond to solutions that are constant in time.

$$\mathbf{Y}(t, \mathbf{Y}^*) \equiv \mathbf{Y}^*.$$

Equilibria may be isolated points or even form a continuum in the phase space. A given equilibrium may be *stable*, *asymptotically stable* or *unstable*, according with the following

Definition A.1. A given equilibrium \mathbf{Y}^* is said to be

- **stable**, if for any $\varepsilon > 0$ it exists δ such that

$$|\mathbf{Y}_0 - \mathbf{Y}^*| < \delta \implies |\mathbf{Y}(t, 0, \mathbf{Y}_0) - \mathbf{Y}^*| < \varepsilon \quad \text{for } t \geq 0;$$

- **asymptotically stable**, if it is stable and there exists δ such that

$$|\mathbf{Y}_0 - \mathbf{Y}^*| < \delta \implies \lim_{t \rightarrow +\infty} \mathbf{Y}(t, 0, \mathbf{Y}_0) = \mathbf{Y}^*;$$

- **unstable** if it is not stable.

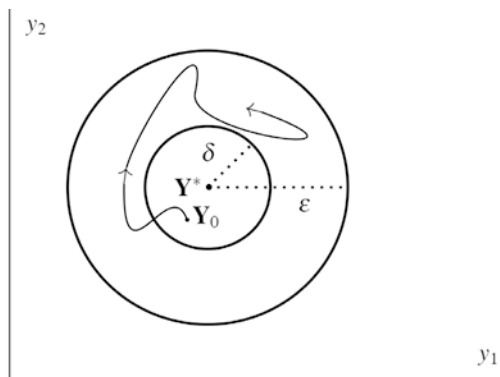


Fig. A.1 Stability of the equilibrium \mathbf{Y}^* . For a fixed circle of radius $\varepsilon > 0$ we find a circle with radius δ such that the trajectories starting inside the latter do not exit from the former

This definition is illustrated in the picture sketched in Fig. A.1. Actually we should specify that this definition concerns the *future* behavior of the solution, since we consider positive times $t > 0$. However we have the same definition concerning *stability in the past*.

These definitions can be soon applied to the one-dimensional case of a scalar equation

$$y'(t) = F(y(t)). \quad (\text{A.6})$$

In this case, the stability of an isolated equilibrium y^* (namely a root of the function $F(y)$) is determined by the derivative of $F(y)$ at the point y^* . In fact we have

- if $F'(y^*) < 0$ the equilibrium y^* is asymptotically stable;
- if $F'(y^*) > 0$ it is unstable.

Indeed such a statement can be easily checked since we have complete knowledge of how the solutions of (A.6) behave (see Fig. A.2), however here we have the basic paradigm according to which in a neighborhood of the equilibrium the *deviation* $\omega(t) = y(t) - y^*$ satisfies approximately the equation

$$\omega'(t) = F'(y^*)\omega(t).$$

We note that the previous statement gives only sufficient conditions and if we have $F'(y^*) = 0$ we cannot conclude either for stability nor for instability.

A.3 Linear systems

The analysis of the linear case is especially important not only because it is possible to give a full description of the solutions, but also because, in the nonlinear cases, local analysis in a neighborhood of an equilibrium point resorts on linearization (as in the one dimensional case) to draw conditions for stability.

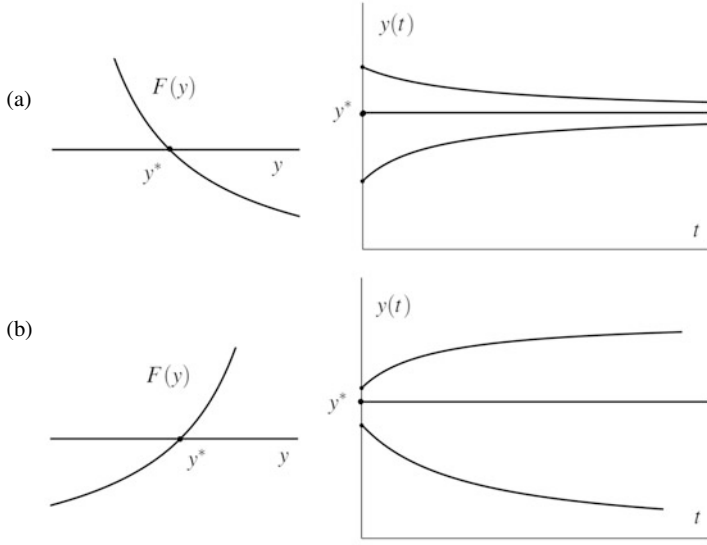


Fig. A.2 The scalar case: stability and instability of an equilibrium point. (a) $F'(y^*) < 0$ and the equilibrium is asymptotically stable; (b) the equilibrium is unstable since $F'(y^*) > 0$

Thus we consider the problem

$$\mathbf{Y}'(t) = A\mathbf{Y}(t), \quad \mathbf{Y}(0) = \mathbf{Y}_0 \quad (\text{A.7})$$

where A is a $n \times n$ matrix. In such a case the origin \mathbf{O} is an equilibrium and the solution can be explicitly expressed through the fundamental solution

$$e^{tA} = \sum_{k=0}^{\infty} \frac{t^k}{k!} A^k \quad \text{as} \quad \mathbf{Y}(t) = e^{tA} \mathbf{Y}_0. \quad (\text{A.8})$$

Going through the Jordan form of A , one can write $\mathbf{Y}(t)$ in terms of the eigenvalues of A . Without going into the details (see [4]), we just state that it is possible to arrive at

$$\mathbf{Y}(t) = \sum_{i=1}^p \sum_{j=0}^{m_i-1} t^j e^{\lambda_i t} \mathbf{v}_{ij} \quad (\text{A.9})$$

where

- λ_i are the eigenvalues of A ($i = 1, \dots, p$);
- m_i is the multiplicity of the eigenvalue λ_i ($i = 1, \dots, p$);
- \mathbf{v}_{ij} are the projection of the initial vector \mathbf{Y}_0 onto the generalized eigenvectors of A ($i = 1, \dots, p$ $j = 0, \dots, m_i - 1$).

Thus we can state

Theorem A.5. *For system (A.7) the origin \mathbf{O} is*

1. *Asymptotically stable, if and only if $\Re\lambda_i < 0$ for all $i = 1, \dots, p$.*
2. *Unstable, if there exists \bar{k} such that $\Re\lambda_{\bar{k}} > 0$.*
3. *Stable, if $\Re\lambda_i \leq 0$ for all $i = 1, \dots, p$, and all eigenvalues with null real part are simple.*

Since each eigenvalue determines a subspace E_i of \mathbb{R}^n with dimension m_i , such that

$$e^{tA}E_i \subset E_i, \quad \mathbb{R}^n = \oplus_i E_i \quad i = 1, \dots, p,$$

we can define three main subspaces E^s, E^c, E^u as

- E^s (stable space), the direct sum of all the E_i with $\Re\lambda_i < 0$;
- E^c (central space), the direct sum of all the E_i with $\Re\lambda_i = 0$;
- E^u (unstable space), the direct sum of all the E_i with $\Re\lambda_i > 0$.

These three spaces are invariant under the matrix e^{tA} and, if \mathbf{Y}_0 belongs to one of them, then in (A.9) only the eigenvalues relative to that space are present. Thus we have

- if $\mathbf{Y}_0 \in E^s$ then $\lim_{t \rightarrow +\infty} |\mathbf{Y}(t, \mathbf{Y}_0)| = 0$ and $\lim_{t \rightarrow -\infty} |\mathbf{Y}(t, \mathbf{Y}_0)| = +\infty$;
- if $\mathbf{Y}_0 \in E^u$ then $\lim_{t \rightarrow -\infty} |\mathbf{Y}(t, \mathbf{Y}_0)| = 0$ and $\lim_{t \rightarrow +\infty} |\mathbf{Y}(t, \mathbf{Y}_0)| = +\infty$;
- if $\mathbf{Y}_0 \in E^c$ then the solution $\mathbf{Y}(t, \mathbf{Y}_0)$ may be constant, run on a circle, or $\lim_{t \rightarrow \pm\infty} |\mathbf{Y}(t, \mathbf{Y}_0)| = +\infty$.

Of course, case (1) of Theorem A.5 corresponds to $E^u \cup E^c = \emptyset$. When $E^s \cup E^c = \emptyset$ the origin \mathbf{O} is said to be *completely unstable*, when $E^s \neq \emptyset$ and $E^u \neq \emptyset$, \mathbf{O} is said to be a *saddle point*. In Fig. A.3 the case of planar systems is illustrated.

By the previous discussion we see that the problem of asymptotic stability of the origin is based on the analysis of the set of the eigenvalues, i.e. on the study of the roots of the characteristic polynomial

$$a_0\lambda^n + a_1\lambda^{n-1} + \dots + a_n. \quad (\text{A.10})$$

In the planar case this polynomial reads

$$\lambda^2 - \text{trace}(A)\lambda + \det(A)$$

and we have

Proposition A.1. *Let A be a 2×2 matrix, then*

- *the origin is asymptotically stable if and only if $\text{trace}(A) < 0$ and $\det(A) > 0$;*
- *if $\det(A) < 0$, then the origin is a saddle point;*
- *if $\det(A) > 0$ and $\text{trace}(A) > 0$, then the origin is completely unstable.*

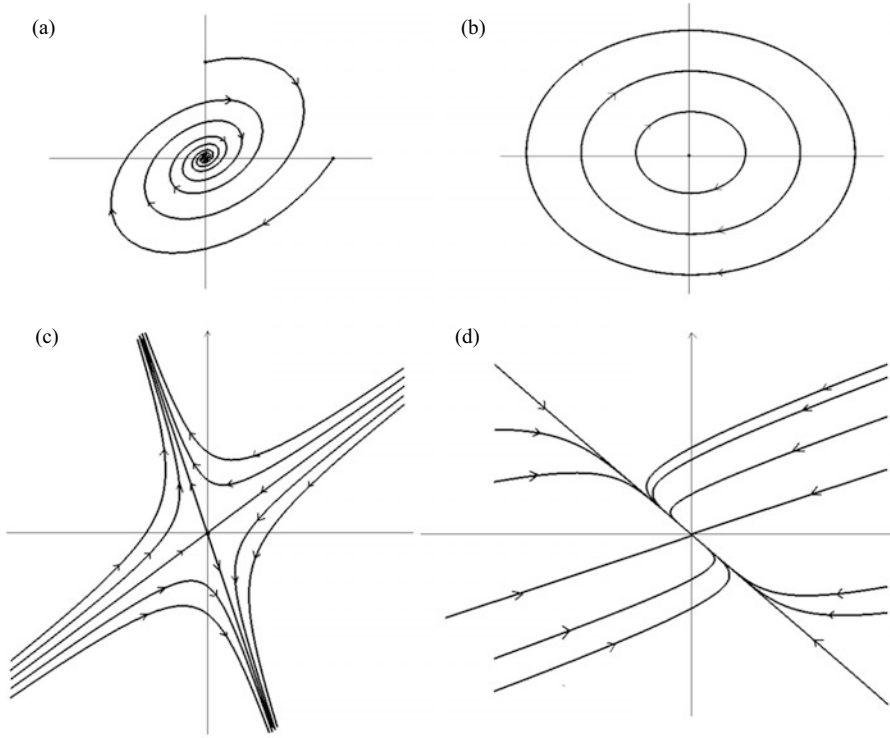


Fig. A.3 Phase plane pictures for linear planar systems. The main cases of stable points: a *focus* (a); a *center* (b); a *saddle point* (c); a *node* (d)

The general n -dimensional case can be systematically approached through the so called *Routh-Hurwitz criterion*. This is based on the $n \times n$ matrix $((H_{ij}))$ built from (A.10) by setting

$$H_{ij} = \begin{cases} a_{2i-j} & \text{if } 0 < 2i - j \leq n, \\ 0 & \text{otherwise.} \end{cases}$$

then we have

Theorem A.6. *All the roots of the polynomial (A.10), with $a_0 > 0$, have negative real part if and only if the principal minors of $((H_{ij}))$ are all positive.*

In the case $n = 3$ the Routh-Hurwitz matrix reads

$$\begin{pmatrix} a_1 & a_0 & 0 \\ a_3 & a_2 & a_1 \\ 0 & 0 & a_3 \end{pmatrix}$$

so that we have the conditions

$$a_0 > 0, \quad a_1 > 0, \quad a_3 > 0, \quad a_1 a_2 - a_0 a_3 > 0. \quad (\text{A.11})$$

Applying this criterion, a condition can be drawn basing on the matrix itself. In fact for a 3×3 matrix A , the characteristic polynomial reads

$$\lambda^3 - \text{trace}(A) \lambda^2 + \sum_{i=1}^3 M_i \lambda - \det(A) = 0$$

where M_i are the three principal minor of order 2. Then, applying (A.11) we have

Proposition A.2. *For a 3×3 matrix A , all eigenvalues have negative real part if and only if*

$$\text{trace}(A) < 0, \quad \det(A) < 0, \quad \text{trace}(A) \sum_{i=1}^3 M_i < \det(A)$$

where M_i are the principal minor of order 2.

The following simple fact is sometimes useful when studying bifurcations (see next section) of 3-dimensional systems. Consider a 3rd-order equation

$$\lambda^3 + a_1(\alpha) \lambda^2 + a_2(\alpha) \lambda + a_3(\alpha) = 0 \quad (\text{A.12})$$

whose coefficients depend continuously on the parameter α .

Assume that the equation satisfies the conditions (A.11) for $\alpha < \alpha^*$ [or $\alpha > \alpha^*$], while they are violated at $\alpha = \alpha^*$. Then, either $a_3(\alpha^*) = 0$ in which case 0 is a root of (A.12) for $\alpha = \alpha^*$; or $a_1(\alpha^*) a_2(\alpha^*) - a_3(\alpha^*) = 0$, in which case (A.12) has two purely imaginary roots at $\alpha = \alpha^*$.

The behavior of the solution of a linear system can also be described in the non autonomous case

$$\mathbf{Y}'(t) = A(t) \mathbf{Y}(t), \quad \mathbf{Y}(0) = \mathbf{Y}_0 \quad (\text{A.13})$$

where now the matrix $A(t)$ is continuous and periodic in time

$$A(t) = A(t + T)$$

where T is the period. In fact, also in this case we have a useful form for the fundamental solution (see [2]):

Theorem A.7 (Floquet Theorem). *Let $A(t)$ be continuously periodic in time with period T , then there exist a matrix $P(t)$, continuously periodic in time with period T , and a constant matrix R , such that the fundamental solution of (A.13) is given by*

$$P(t) e^{tR}.$$

Thus the solution of (A.13) can be expressed as

$$\mathbf{Y}(t) = P(t)e^{tR}\mathbf{Y}_0$$

and the eigenvalues of the matrix R determine the asymptotic behavior. These eigenvalues z_i are traditionally called the *characteristic exponents* of system (A.13). Instead, the eigenvalues μ_i of the matrix e^{TR} are called the *Floquet multipliers* of the system. And we have

$$\mu_i = e^{Tz_i}.$$

A.4 The non-linear case

The results of the previous section provide the key to approach the non-linear case. We consider the following autonomous system

$$\mathbf{Y}'(t) = A\mathbf{Y}(t) + \mathbf{G}(\mathbf{Y}(t)), \quad (\text{A.14})$$

where A is a $n \times n$ matrix and $\mathbf{G} : \mathbb{R}^n \rightarrow \mathbb{R}^n$ is continuously differentiable and

$$\lim_{\mathbf{x} \rightarrow \mathbf{0}} \frac{|\mathbf{G}(\mathbf{x})|}{|\mathbf{x}|} = 0 \quad (\text{A.15})$$

Then the origin $\mathbf{0}$ is an equilibrium for (A.14) and we have

Theorem A.8. *Consider system (A.14) and let $\lambda_1, \dots, \lambda_p$ be the eigenvalues of the matrix A . We have*

- if $\Re \lambda_i < 0$ for all $i = 1, \dots, p$, then the origin $\mathbf{0}$ is asymptotically stable;
- if there exist k such that $\Re \lambda_k > 0$, then the origin $\mathbf{0}$ is unstable.

This result can be actually applied to the stability analysis of equilibria of system (A.5), because if \mathbf{Y}^* is such an equilibrium, we consider the deviation

$$\mathbf{W}(t) = \mathbf{Y}(t, \mathbf{Y}_0) - \mathbf{Y}^*$$

which is a solution of the linearized system

$$\mathbf{W}'(t) = \mathbf{JF}(\mathbf{Y}^*)\mathbf{W}(t) + \mathbf{G}(\mathbf{W}(t)), \quad \mathbf{W}(0) = \mathbf{Y}_0 - \mathbf{Y}^*, \quad (\text{A.16})$$

where $\mathbf{JF}(\mathbf{Y}^*)$ is the Jacobian matrix of \mathbf{F} at the equilibrium and $\mathbf{G}(\cdot)$ the remainder, satisfying (A.15). Indeed we have

Theorem A.9. *Consider system (A.5) and an equilibrium \mathbf{Y}^* . let $\lambda_1, \dots, \lambda_p$ be the eigenvalues of the Jacobian $\mathbf{JF}(\mathbf{Y}^*)$ at \mathbf{Y}^* . We have*

- if $\Re \lambda_i < 0$ for all $i = 1, \dots, p$, then \mathbf{Y}^* is asymptotically stable;
- if there exist k such that $\Re \lambda_k > 0$, then \mathbf{Y}^* is unstable.

We stress the local nature of the previous result and also note that the critical cases, when one or more eigenvalues have null real part, are not decidable on the basis of the linearization.

A few additional results are in order. First we have

Theorem A.10. *If \mathbf{Y}^* is unstable with $\Re \lambda_i > 0$ for all $i = 1, \dots, p$, then \mathbf{Y}^* is said to be **completely unstable** and there exists $\delta > 0$ such that, for any \mathbf{Y}_0 satisfying $|\mathbf{Y}_0 - \mathbf{Y}^*| < \delta$, there exist $T > 0$ such that*

$$|\mathbf{Y}(t, \mathbf{Y}_0) - \mathbf{Y}^*| > \delta \quad \text{for all } t > T.$$

Then we consider the case of a *saddle point*, i.e. the case when the Jacobian $\mathbf{JF}(\mathbf{Y}^*)$ has both eigenvalues with positive real part and eigenvalues with negative real part. We have

Theorem A.11. *If \mathbf{Y}^* is a saddle point with no eigenvalues with null real part, then there exist two invariant differential manifolds $\mathcal{M}^s(\mathbf{Y}^*)$ and $\mathcal{M}^u(\mathbf{Y}^*)$ with the following properties*

- $\mathcal{M}^s(\mathbf{Y}^*)$ and $\mathcal{M}^u(\mathbf{Y}^*)$ are respectively tangent to E^s and E^u at \mathbf{Y}^* ;
- there exist a neighborhood \mathcal{U} of \mathbf{Y}^* such that

$$\mathcal{M}^s(\mathbf{Y}^*) = \left\{ \mathbf{x} \in U \mid \lim_{t \rightarrow +\infty} \mathbf{Y}(t, \mathbf{x}) = \mathbf{Y}^* \quad \text{and} \quad \mathbf{Y}(t, \mathbf{x}) \in \mathcal{U} \quad \text{for } t \geq 0 \right\},$$

$$\mathcal{M}^u(\mathbf{Y}^*) = \left\{ \mathbf{x} \in U \mid \lim_{t \rightarrow -\infty} \mathbf{Y}(t, \mathbf{x}) = \mathbf{Y}^* \quad \text{and} \quad \mathbf{Y}(t, \mathbf{x}) \in \mathcal{U} \quad \text{for } t \leq 0 \right\}.$$

The two manifolds are respectively named *stable manifold* and *unstable manifold*. In Fig. A.4 a few example are shown in the planar case to illustrate the previous concepts.

The method presented above, based on the linearization of the original problem to obtain results on the stability of equilibria, can be pushed forward and include stability of periodic orbits. In this case we consider a closed orbit Γ , parametrized through the periodic solution $\mathbf{P}(t)$, and take the deviation

$$\mathbf{W}(t) = \mathbf{Y}(t, \mathbf{Y}_0) - \mathbf{P}(t), \quad \mathbf{W}(0) = \mathbf{Y}_0 - \mathbf{P}(0).$$

Then linearization of the autonomous problem (A.5) leads to the non autonomous linear problem

$$\mathbf{W}'(t) = \mathbf{JF}(\mathbf{P}(t))\mathbf{W}(t), \quad \mathbf{W}(0) = \mathbf{Y}_0 - \mathbf{P}(0), \quad (\text{A.17})$$

where the matrix $\mathbf{JF}(\mathbf{P}(t))$ is periodic. In this case we resort on Floquet theory (see Theorem A.7) and we need to consider the Floquet multipliers to discuss stability of Γ . As $\mathbf{W}(t)$ represents the deviation for a periodic orbit, one of the multipliers is 1. Hence Γ is asymptotically stable if all the other multipliers μ_i satisfy $|\mu_i| < 1$ and is unstable if at least one of them satisfies $|\mu_i| > 1$. Explicit formulae for the Floquet

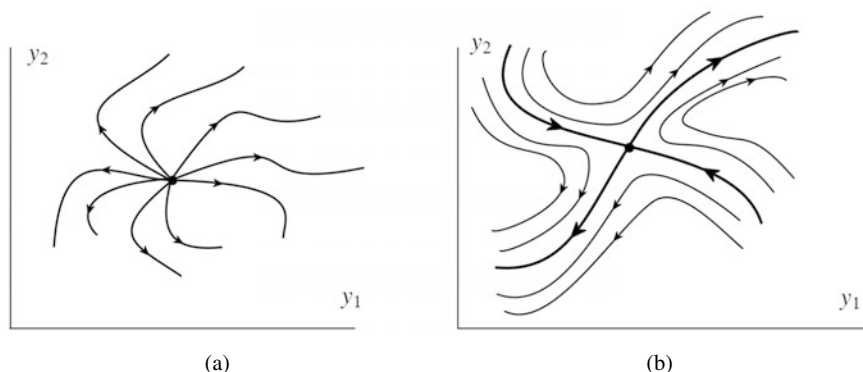


Fig. A.4 Phase plane pictures for nonlinear planar systems. (a) approximate picture of a *completely unstable* node; (b) approximate picture of a saddle node: here the two curves pointing to the equilibrium are the *stable manifold*, while the two curves exiting from the equilibrium are the *unstable manifold*

multipliers can rarely be obtained, except in some special cases as the one treated in Sect. 9.2, and one generally has to rely on numerical computations or clever arguments.

A.5 Limit sets

The previous results concern the behavior of the solutions in a neighborhood of an equilibrium. Their asymptotic behavior is well determined only when the equilibrium is asymptotically stable. A basic concept for analyzing the behavior of any solution is its ω -limit set

$$\omega(\mathbf{x}) = \{\mathbf{y} \mid \text{there exists } \{t_n\}, \quad t_n \rightarrow +\infty, \quad \mathbf{Y}(t_n, \mathbf{x}) \rightarrow \mathbf{y}\}$$

the relative properties are given in the following Theorem

Theorem A.12. Consider the solution $\mathbf{Y}(t, \mathbf{x})$ and suppose that its positive orbit

$$O_+(\mathbf{x}) = \{\mathbf{Y}(t, \mathbf{x}), t \geq 0\}$$

is bounded. Then

- $\omega(\mathbf{x}) \neq \emptyset$;
- $\omega(\mathbf{x})$ is closed and connected;
- $\omega(\mathbf{x})$ is invariant;
- $\lim_{t \rightarrow +\infty} d(\mathbf{Y}(t, \mathbf{x}), \omega(\mathbf{x})) = 0$;

where $d(\mathbf{x}, \mathbf{y})$ denotes the distance between \mathbf{x} and \mathbf{y} .

The last statement of the Theorem gives a precise account of how the solution tends to $\omega(\mathbf{x})$.

Special cases of ω -limit sets are

- $\omega(\mathbf{x}) = \mathbf{Y}^*$, when \mathbf{Y}^* is an equilibrium and $\lim_{t \rightarrow +\infty} \mathbf{Y}(t, \mathbf{x}) = \mathbf{Y}^*$;
- $\omega(\mathbf{x}) = O_+(\mathbf{x})$ when $\mathbf{Y}(t, \mathbf{x})$ is a periodic solution ($\mathbf{Y}(t, \mathbf{x}) = \mathbf{Y}(t + T, \mathbf{x})$).

The concept of ω -limit set concerns the solution as $t \rightarrow +\infty$, i.e. *in the future*. Of course we can consider the same concept as $t \rightarrow -\infty$ and define the α -limit set

$$\alpha(\mathbf{x}) = \{\mathbf{y} \mid \text{there exists } \{t_n\}, \quad t_n \rightarrow -\infty, \quad \mathbf{Y}(t_n, \mathbf{x}) \rightarrow \mathbf{y}\},$$

concerning the solution *in the past*.

A useful result concerning limit sets is the following (see [9, Sect. 8.2]), known as Butler-McGehee Lemma, that we state in a very simple form, originally due to Freedman and Waltman

Proposition A.3. *Let \mathbf{Y}^* be an isolated equilibrium of (A.20), and let $\mathbf{Y}^* \in \omega(\mathbf{x})$ but $\omega(\mathbf{x}) \neq \mathbf{Y}^*$. Then $\omega(\mathbf{x})$ includes a point $x_1 \in \mathcal{M}^s(\mathbf{Y}^*)$, $x_1 \neq \mathbf{Y}^*$, (hence the whole orbit through x_1) and a point $x_2 \in \mathcal{M}^u(\mathbf{Y}^*)$, $x_2 \neq \mathbf{Y}^*$ (hence the whole orbit through x_2).*

A.6 Planar case: Poincaré-Bendixson theory

In the case of planar systems

$$\begin{aligned} y_1' &= F_1(y_1, y_2), \\ y_2' &= F_2(y_1, y_2), \end{aligned} \tag{A.18}$$

the analysis of the structure of the ω -limit sets is rather clear and is based on the following theorem;

Theorem A.13. *Consider the autonomous system (A.18) and suppose that the orbit $O_+(\mathbf{Y}_0)$ is bounded. If the ω -limit set $\omega(\mathbf{Y}_0)$ does not contain any equilibrium point, then it is a periodic orbit.*

This result has several consequences for planar systems. In fact we have

Theorem A.14. *Consider the autonomous system (A.18) and suppose that there exists a finite number of equilibria. If the orbit $O_+(\mathbf{Y}_0)$ is bounded then we have one of the following statements*

- $\omega(\mathbf{Y}_0)$ is an equilibrium;
- $\omega(\mathbf{Y}_0)$ is a periodic orbit;
- $\omega(\mathbf{Y}_0)$ is a singular cycle, i.e. it is the union of a finite number of orbits joining such points as $t \rightarrow +\infty$ or as $t \rightarrow -\infty$ (either heteroclinic or homoclinic orbits).

The previous theorem restricts the possible outcomes and any information to exclude existence of periodic orbits is very useful. Indeed we have

Theorem A.15 (Bendixson-Dulac criterion). *Consider system (A.18) and suppose that there exist a function $L(y_1, y_2)$ such that*

$$\frac{\partial}{\partial y_1} [L(y_1, y_2)F_1(y_1, y_2)] + \frac{\partial}{\partial y_2} [L(y_1, y_2)F_2(y_1, y_2)] < 0, \quad (\text{or } > 0)$$

in an open region Ω . Then no periodic orbits or singular cycles exist in Ω .

Finally, a simple statement that may help is the following

Theorem A.16. *For system (A.18), the region enclosed by a periodic orbit must contain at least one equilibrium.*

A.7 Planar competitive and cooperative systems

A class of differential equations for which a large body of theory has been developed is that of cooperative or competitive systems. An extensive account of the theory, not limited to differential equations, including many results of interest for Population Dynamics can be found in [8].

In the general case of problem (A.1) with (A.2) we have the following

Definition A.2. The system (A.1) with (A.2) is said to be *competitive* if

$$\frac{\partial F_i}{\partial x_j} < 0 \quad \text{for } i \neq j$$

it is said to be *cooperative* if, instead,

$$\frac{\partial F_i}{\partial x_j} > 0 \quad \text{for } i \neq j.$$

The class of competitive systems fits exactly the class of models designed to describe competition, as those we have considered in Chap. 7.

We limit ourselves to consider planar systems, for which a simple result holds, allowing to determine the global asymptotic behavior of the solutions. In fact we have

Theorem A.17. *For a planar competitive system, all the solutions are eventually monotone. Then any bounded solutions goes to an equilibrium point as $t \rightarrow +\infty$.*

The same result holds for a cooperative system that in fact can be easily changed into a competitive one through the transformation

$$F_1 \rightarrow \tilde{F}_1(x_1, x_2) = F_1(x_1, -x_2), \quad F_2 \rightarrow \tilde{F}_2(x_1, x_2) = -F_2(x_1, -x_2).$$

A.8 Lyapunov functions

A wide range of results concerning the qualitative behavior of solutions to Problem (A.5) resort on the use of Lyapunov functions that provide an alternative method to investigate stability. To present the results we first consider a continuously differentiable function $V(\mathbf{x}) : \mathbb{R}^n \rightarrow \mathbb{R}$ and, referring to (A.5), we define

$$\dot{V}(\mathbf{x}) \equiv \dot{V}(x_1, \dots, x_n) = \sum_{i=1}^n \frac{\partial}{\partial x_i} V(x_1, \dots, x_n) F_i(x_1, \dots, x_n).$$

Then we have

Theorem A.18 (Lyapunov theorem). *Let \mathbf{Y}^* be an equilibrium for system (A.5), and suppose there exist a continuously differentiable function $V(\mathbf{x})$ defined in a neighborhood \mathcal{U} of \mathbf{Y}^* , such that*

- $V(\mathbf{Y}^*) = 0$;
- $V(\mathbf{x}) > 0$ for $\mathbf{x} \in \mathcal{U}$ and $\mathbf{x} \neq \mathbf{Y}^*$;
- $\dot{V}(\mathbf{x}) \leq 0$ on \mathcal{U} ;

then \mathbf{Y}^ is stable. If moreover*

- $\dot{V}(\mathbf{x}) < 0$ for $\mathbf{x} \neq \mathbf{Y}^*$,

then \mathbf{Y}^ is asymptotically stable.*

Finally, information about the ω -limit set come from the following result:

Theorem A.19 (La Salle theorem). *Consider system (A.5) and suppose it exists a continuously differentiable function $V(\mathbf{x})$, defined on a positively invariant region Ω and such that*

$$\dot{V}(\mathbf{x}) \leq 0, \quad \text{for all } \mathbf{x} \in \Omega.$$

Then, for any $\mathbf{Y}_0 \in \Omega$, we have

$$\omega(\mathbf{Y}_0) \subset \{\mathbf{x} \in \Omega \mid \dot{V}(\mathbf{x}) = 0\}.$$

A.9 Persistence

The theory, and the concept itself, of persistence developed in the last few decades, and constitutes now an important method for analyzing population dynamics models. An extensive and clear account of the theory can be found in the book by Smith and Thieme [9]. Here we restrict ourselves to the very few results we used in this book, and that we feel essential.

Consider a system

$$\mathbf{Y}'(t) = \mathbf{F}(\mathbf{Y}(t)) \quad \text{with} \quad F_i(\mathbf{Y}) = y_i f_i(\mathbf{Y}) \quad (\text{A.19})$$

and f_i defined and regular on the non-negative orthant. Note that all the hyperplanes $\{y_i = 0\}$ are invariant for system (A.19)

Definition A.3. System (A.19) is persistent if there exists $\varepsilon > 0$ such that

$$\text{if } \mathbf{Y}_0 \text{ satisfies } \min_{i=1\dots n} (Y_0)_i > 0, \text{ then } \liminf_{t \rightarrow \infty} y_i(t) \geq \varepsilon$$

where $\mathbf{Y}(t; \mathbf{Y}_0) = (y_1(t), \dots, y_n(t))$ is the solution of (9.5) with $\mathbf{Y}(0) = \mathbf{Y}_0$. It is weakly uniformly persistent if there exists $\varepsilon > 0$ such that

$$\text{if } \mathbf{Y}_0 \text{ satisfies } \min_{i=1\dots n} (Y_0)_i > 0, \text{ then } \limsup_{t \rightarrow \infty} y_i(t) \geq \varepsilon.$$

We take from [9] two results simplified to suit system (A.19). Before stating the theorems, some definitions are needed.

Let X_0 be the boundary of \mathbb{R}_+^n , i.e. the union of all coordinate hyperplanes. A set $M \subset X_0$ is named weakly repelling if there exists $\varepsilon > 0$ such that, for all strictly positive x ,

$$\limsup_{t \rightarrow \infty} d(Y(t; x), M) \geq \varepsilon.$$

Note that, if M is a hyperbolic equilibrium, it is *weakly repelling* if its stable manifold has no intersection with the interior of \mathbb{R}_+^n .

Finally, a collection $\{M_1, \dots, M_n\}$ of subsets of X_0 is *cyclic* if, after possibly renumbering the sets, there exist $y_{12}(t)$, $y_{23}(t)$, \dots , $y_{n-1,n}(t)$, $y_{n,1}(t)$ solutions of (A.19) belonging to X_0 such that $\lim_{t \rightarrow -\infty} d(y_{ij}, M_i) = 0$, $\lim_{t \rightarrow +\infty} d(y_{ij}, M_j) = 0$. If $\{M_1, \dots, M_n\}$ is not cyclic, it is *acyclic*.

Theorem A.20 (Theorem 8.17 in [9]). Let $\cup_{x \in X_0} \omega(x) = \cup_{i=1}^n M_i$ where each M_i is isolated, compact and weakly repelling. If $\{M_1, \dots, M_n\}$ is acyclic, then (A.19) is weakly uniformly persistent.

A second very useful result is the following

Theorem A.21 (Theorem 4.5 in [9]). Assume there exists a compact set B such that for each strictly positive x

$$\lim_{t \rightarrow \infty} d(Y(t; x), B) = 0.$$

Then if (A.19) is weakly uniformly persistent, it is persistent.

The two Theorems can be combined in the following result

Theorem A.22. Assume there exists a compact set B such that for each strictly positive x

$$\lim_{t \rightarrow \infty} d(Y(t; x), B) = 0.$$

Let $\cup_{x \in X_0} \omega(x) = \cup_{i=1}^n M_i$ where each M_i is isolated, compact and weakly repelling. If $\{M_1, \dots, M_n\}$ is acyclic, then (A.19) is persistent.

A.10 Elementary bifurcations

Bifurcation theory (here presented for ordinary differential equations, but similar concepts hold for much more general classes of equation) concerns families of dif-

ferential equations depending on a parameter α (here taken in \mathbb{R})

$$\mathbf{Y}'(t) = \mathbf{F}(\alpha, \mathbf{Y}(t)), \quad (\text{A.20})$$

where $\mathbf{Y}(t) \in \mathbb{R}^n$, and $\mathbf{F}(\cdot, \cdot)$ is regular enough (we do not go in details here).

The theory examines the possible changes in the qualitative structure of the system, as the parameter α varies. We refer to [6] (more elementary and computational) or [10] for a comprehensive introduction to the topic. Here we present simply the recipes for the simplest (and common in mathematical biology) equilibrium bifurcations. Equilibrium bifurcation means qualitative changes that relate to changes in the properties of an equilibrium of system (A.20).

Correspondingly to the family of differential equations (A.20), we will consider family of equilibria \mathbf{Y}_α depending on α ; as seen above, its stability properties, are determined by the real sign of eigenvalues of the Jacobian matrix $\mathbf{J}(\alpha) = \mathbf{JF}(\alpha, \mathbf{Y}_\alpha)$. Neglecting cases where system (A.20) has eigenvalues with 0 real part for all α in an interval (bifurcation theory considers only generic properties, which intuitively means for almost all systems), changes in stability may occur only when one eigenvalue crosses the imaginary axis at some value α^* .

We then consider 3 cases, discussed in greater detail below:

- **tangent bifurcation** $\mathbf{J}(\alpha^*)$ has eigenvalue 0 and $\mathbf{F}_\alpha(\alpha^*, \mathbf{Y}_{\alpha^*}) \neq 0$;
- **transcritical bifurcation** $\mathbf{J}(\alpha^*)$ has eigenvalue 0 but $\mathbf{F}_\alpha(\alpha^*, \mathbf{Y}_{\alpha^*}) = 0$;
- **Hopf bifurcation** $\mathbf{J}(\alpha^*)$ has eigenvalues $\pm i\omega$ (necessarily $n \geq 2$).

Tangent bifurcation. A one dimensional prototype for this case is the equation

$$y'(t) = F(\alpha, y(t)) = \alpha - y^2(t). \quad (\text{A.21})$$

Here we have the two branches of equilibria

$$y_\pm^*(\alpha) = \pm\sqrt{\alpha}$$

existing only for $\alpha \geq 0$. At $\alpha = 0$ we have $F_x(0, 0) = 0$ and $F_\alpha(0, 0) = 1$, thus $\alpha = 0$ is the bifurcation point and for $\alpha > 0$ we have $F_x(\alpha, y_\pm^*(\alpha)) = \mp 2\sqrt{\alpha}$, thus $y_+^*(\alpha)$ is asymptotically stable, $y_-^*(\alpha)$ unstable.

More generally, when some other technical conditions hold, (A.20) has two equilibria in a neighborhood U of \mathbf{Y}_{α^*} for $\alpha < \alpha^*$ and none for $\alpha > \alpha^*$, or vice versa. Furthermore, one equilibrium will have k eigenvalues with negative real part (and $n - k$ with positive), and the other one $k - 1$, with $1 \leq k \leq n$; if $k = n$, one equilibrium is asymptotically stable, and the other one is unstable.

Transcritical bifurcation. The one dimensional prototype in this case is

$$y'(t) = (\alpha - y(t))y(t), \quad (\text{A.22})$$

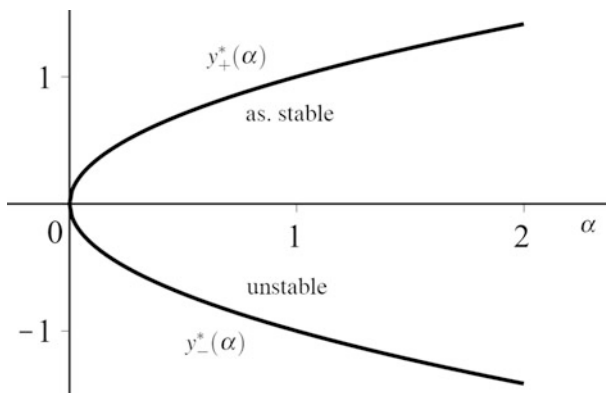


Fig. A.5 Tangent bifurcation: the prototype example (A.21). The two branches $y_+^*(\alpha)$ and $y_-^*(\alpha)$, originating at $\alpha = 0$, are shown together with their stability

and we have the equilibria

$$y_0^*(\alpha) = 0, \quad y^*(\alpha) = \alpha.$$

Now, at $\alpha = 0$ we have $F_x(0,0) = 0$, but $F_\alpha(0,0) = 0$. For $\alpha < 0$, the equilibrium $y_0^*(\alpha)$ is asymptotically stable because $F_x(\alpha, y_0^*(\alpha)) = \alpha$ and the equilibrium α is unstable because $F_x(\alpha, \alpha) = -\alpha$; for $\alpha > 0$ vice versa.

The fact that $\mathbf{F}_\alpha = 0$ can be considered to be non-generic, but many classes of systems in mathematical population dynamics share the property that one state (that we call 0, thinking of population density) is an equilibrium for all parameter values. If the model has a biological interpretation, negative values are often not considered, so that the equilibrium α is neglected for $\alpha < 0$. In this light, the transcritical bifurcation can be viewed not as an intersection of two equilibria that exchange their stability, but as the emergence of a new equilibrium at $\alpha = 0$, as the equilibrium 0 loses its stability.

In this interpretation, one can distinguish a forward and a backward bifurcation; in the forward bifurcation (case above), the new equilibrium exists when 0 is unstable and inherits its stability; a backward bifurcation is exemplified by the equation $y'(t) = (\alpha + y(t))y(t)$, in which a positive equilibrium $-\alpha$ exists when the equilibrium 0 is asymptotically stable and is unstable. We insist that this distinction depends on the choice of restricting the system to one side of the 0 equilibrium.

More generally, without pursuing this distinction (see, for instance, [1]), a transcritical bifurcation may occur in systems where a state, say \mathbf{O} , is an equilibrium for α . Assume then $\mathbf{F}(\alpha, \mathbf{O}) = 0 \forall \alpha$, and assume that $\mathbf{J}(\alpha)$ has eigenvalue 0 at α^* and (to be definite) k eigenvalues with negative real part (and $n - k$ with positive) for $\alpha < \alpha^*$, and $k - 1$ eigenvalues with negative real part for $\alpha > \alpha^*$. Under some other technical conditions, there exists another branch of equilibria Y_α for α close to α^* , crossing 0 at α^* , such that $\mathbf{J}(\alpha)$ has $k - 1$ eigenvalues with negative real part for $\alpha < \alpha^*$ and k for $\alpha > \alpha^*$.

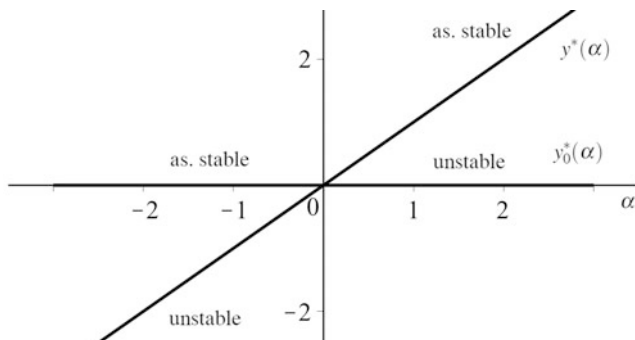


Fig. A.6 Transcritical bifurcation: the prototype (A.22). Here the two branches $y_0^*(\alpha)$ and $y^*(\alpha)$ exist for all values of α and cross at $\alpha = 0$ exchanging their stability

Hopf bifurcation.

In this case the prototype is two-dimensional:

$$\begin{cases} y_1' = -y_2 + (\alpha \pm (y_1^2 + y_2^2))y_1 \\ y_2' = y_1 + (\alpha \pm (y_1^2 + y_2^2))y_2 \end{cases}. \quad (\text{A.23})$$

The origin $(0,0)$ is an equilibrium for all values of α , and its Jacobian has eigenvalues $\alpha \pm i$; hence they have negative real part for $\alpha < 0$, positive real part for $\alpha > 0$, while they are purely imaginary for $\alpha = 0$.

It is convenient to look at the same system in polar coordinates

$$\begin{cases} \dot{\rho} = (\alpha \pm \rho^2)\rho \\ \dot{\vartheta} = 1 \end{cases}.$$

In fact, in this way it is clear that the properties of the system depend crucially on whether there is $+$ or $-$ in front of ρ^2 ; there are actually two types of Hopf bifurcation, *supercritical* (corresponding to the case with a $-$) and *subcritical* (corresponding to the case with a $+$). In the former case, $(0,0)$ is asymptotically stable also for $\alpha = 0$ and, for all $\alpha > 0$, there exist an attracting periodic orbit

$$\rho(t) \equiv \sqrt{\alpha}, \quad \vartheta(t) = t,$$

while there are no periodic orbits for $\alpha < 0$. In the latter, $(0,0)$ is unstable also for $\alpha = 0$ and, for all $\alpha < 0$, there exist a repulsive periodic orbit

$$\rho(t) \equiv \sqrt{-\alpha}, \quad \vartheta(t) = t$$

while there are no periodic orbits for $\alpha > 0$.

In general, assume that there exists a branch of equilibria \mathbf{Y}_α of (A.20) such that the Jacobian has k eigenvalues with negative real part (and $n - k$ with positive) for $\alpha < \alpha^*$, while $k - 2$ with negative real part (and $n + 2 - k$ with positive) for $\alpha > \alpha^*$.

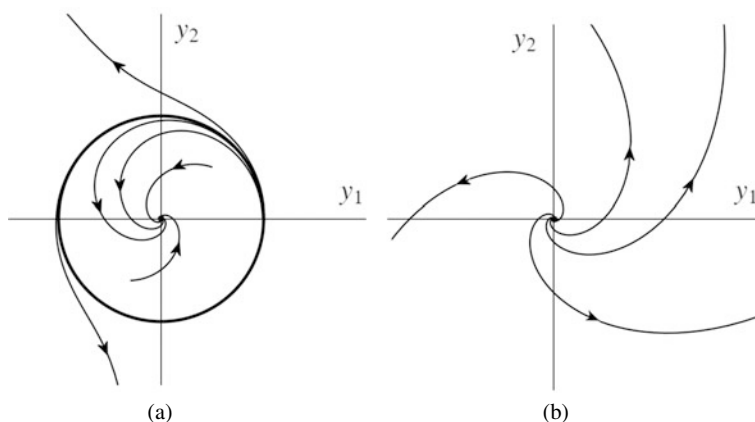


Fig. A.7 Hopf bifurcation for prototype (A.23) in the *subcritical* case. Here the origin $(0,0)$ is an equilibrium for all values of α : (a) for $\alpha < 0$ the origin is asymptotically stable and there exists a *repulsive* periodic orbit; (b) if $\alpha > 0$ there are no periodic orbits close to the origin and the origin is repulsive. The radius of the periodic orbit, when it exists, is $\rho(\alpha) = \sqrt{-\alpha}$, it bifurcates from the origin as α crosses backward the value $\alpha = 0$

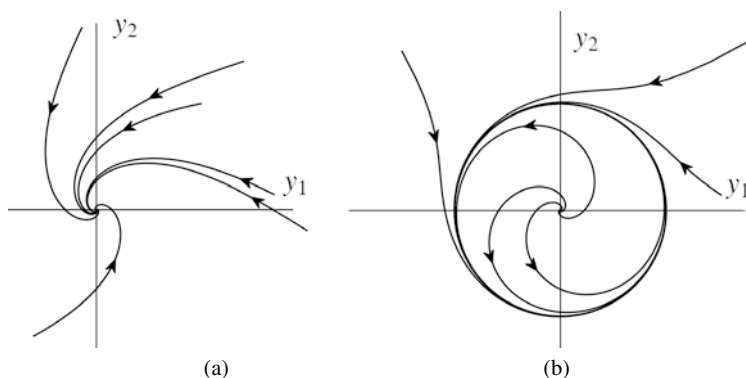


Fig. A.8 Hopf bifurcation for prototype (A.23) in the *supercritical* case. Here the origin $(0,0)$ is an equilibrium for all values of α . For $\alpha < 0$ (a) the origin is globally attractive. As α crosses forward the value $\alpha = 0$, a periodic orbit bifurcates, with radius $\rho(\alpha) = \sqrt{\alpha}$, inheriting the stability of the origin (b)

Finally assume that the Jacobian at α^* has eigenvalues $\pm i\omega$ with $\omega > 0$, while all other eigenvalues have non-zero real part. Necessarily it must be $n \geq k \geq 2$.

Under some technical conditions, one can compute a quantity a_0 (see, for instance, (5.62) in [6]) such that if $a_0 \neq 0$, there exist a family of periodic orbits $\Gamma(\alpha)$ contracting to $\mathbf{Y}(\alpha^*)$ as α approaches α^* . If $a_0 < 0$ (supercritical Hopf bifurcation), $\Gamma(\alpha)$ exists for $\alpha > \alpha^*$ (and close to α^*) and its stable manifold has dimension k (if $k = n$, i.e. $x^*(\alpha)$ is asymptotically stable, for $\alpha < \alpha^*$, the periodic orbit is attracting). If $a_0 > 0$ (subcritical Hopf bifurcation), $\Gamma(\alpha)$ exists for $\alpha < \alpha^*$ (and close to α^*) and its stable manifold has dimension $k - 2$ (thus, the periodic orbit is unstable).

We end this section by remarking that all these results are local: they depend only on the values of the function in a neighborhood of the equilibria, and they describe the behavior of the solutions only in the neighborhood. This is the reason why in the text we generally relied on methods that could yield the global structure of the solutions. However, local bifurcation theory is a very effective method to explore (especially through numerical bifurcation tools such as AUTO or MATCONT) the (local) behavior of a system, and also to get some insights into the global behavior.

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Appendix B

Delay Equations

As we already noted at the beginning of Chap. 2, the need of introducing delays in the description of natural phenomena was clearly stated early in the past century and a first important contribution was due to Vito Volterra in the field of the class of equations that, after him, are actually named Volterra Equations (see [7] and the brief historical review in [1]). However, delay equations, in the case of concentrated delays as well as of distributed delays, in their classical form or in the abstract context of Functional Differential Equations, have an extensive development starting with the 1950's. This appendix is mainly designed to meet the needs arising in the context of the basic models discussed in Chap. 2 and provides a minimal pathway through the subject. The reader may refer to [2, 3, 6] for a full treatment.

B.1 On the nature of delay equations

In general, a delay equation with *concentrated delay* has the form

$$\begin{cases} y'(t) = F(y(t), y(t - \tau)), & t > 0 \\ y(t) = \phi(t), & t \in [-\tau, 0], \end{cases} \quad (\text{B.1})$$

where τ is the *delay* and $\phi(t)$ represents a given *initial heredity*. This particular kind of equation can be solved by the so-called *method of steps*, namely a solution can be built piecewise in each interval

$$I_i = ((i - 1)\tau, i\tau], \quad i = 0, 1, 2, \dots,$$

knowing the solution in the previous interval I_{i-1} . In fact we build the sequence $y_i(t)$, starting with

$$y_0(t) = \phi(t), \quad t \in I_0$$

and from $y_{i-1}(t)$ defined in I_{i-1} we get $y_i(t)$ in I_i solving

$$\begin{cases} y'_i(t) = F(y_i(t), y_{i-1}(t - \tau)), & t \in I_i \\ y_i((i - 1)\tau) = y_{i-1}((i - 1)\tau). \end{cases}$$

On the other hand, the case of *distributed delays* corresponds to an *integro-differential equations* of Volterra type and can be represented by the rather general form

$$ay'(t) = F\left(y(t), \int_{-\infty}^t K(t-s)y(s) ds\right), \quad y(t) = \phi(t), \quad t \in (-\infty, 0], \quad (\text{B.2})$$

that, for $a = 0$, includes the case of *integral equations*. Often in (B.2) the kernel is normalized

$$\int_0^{+\infty} K(s)ds = 1, \quad (\text{B.3})$$

so that the scaling is left to some parameter included in the equation.

Though in this case the method of steps does not work, existence and uniqueness of a solution can be proved by fixed point procedures and similar arguments holding for Ordinary Differential Equations. In both cases, the problem of determining the asymptotic behavior of the solution is somewhat more difficult and tricky than in the case of ordinary differential equations.

B.2 Linear delay equations

The linear case of eq. (B.1) has the form

$$\begin{cases} y'(t) = ay(t) + by(t - \tau), & t > 0 \\ y(t) = \phi(t), & t \in [-\tau, 0], \end{cases}$$

where a and b are real numbers. As we have shown before, the method of steps provides a solution for all times $t > 0$ and some cases have been considered in Chap. 2. Concerning the asymptotic behaviour of this solution, a classical method resorts on Laplace transform that provides the formal series

$$y(t) \equiv \sum_0^{+\infty} p_i(t)e^{\lambda_i t} \quad (\text{B.4})$$

where $p_i(t)$ are polynomials and λ_i are the roots of the characteristic equation

$$\lambda = a + be^{-\lambda\tau}, \quad (\text{B.5})$$

namely the singularities of the Laplace transform

$$\widehat{y}(\lambda) = \frac{y(0)}{\lambda - a - be^{-\lambda\tau}}.$$

The polynomial $p_i(t)$ depends on the multiplicity of the corresponding root λ_i .

Actually the roots of (B.5) correspond to an infinite set of exponential solutions $e^{\lambda_i t}$ that provide the formal series solution (B.4) and allow conclusions on the asymptotic behavior. In fact, by the knowledge of these roots and the use of the inverse

Laplace transform theorem, the formal series (B.4) can be given the meaning of an *asymptotic expansion*, i. e. it is possible to prove that

$$y(t) = \left(\sum_0^N p_i(t) e^{\lambda_i t} \right) (1 + \Omega(t)) \quad \text{with} \quad \lim_{t \rightarrow +\infty} \Omega(t) = 0$$

for some N as large as we want.

In Sect. 2.2 we have considered a case in which the method has given significant results. For the details of this procedure we recommend classical references like [2] and [4] where the interested reader can also find examples and applications to cases that go beyond the problems treated in Chap. 2. In fact, the study of existence and location of the roots of an *exponential polynomial*, namely the study of equations like

$$\sum_{i=1}^n P_i(\lambda) e^{-\tau_i \lambda} = 0$$

where $P_i(\lambda)$ is a polynomial, is a classical subject related to the study of systems of delayed equations in the three classes of *retarded*, *neutral* and *advanced* equations, with multiple delays. Basic results on this equations are presented in classical treatises such as [1]. In particular, the single first order delayed equation leads to the study of

$$a_0 \lambda + b_0 + (a_1 \lambda + b_1) e^{-\tau \lambda} = 0 \quad (\text{B.6})$$

for which it is possible to state that the the roots are approximately located on the curve shown in Fig. B.1.

Another source of transcendental characteristic equations are systems of integral and integro-differential equations of Volterra type, such as (2.4) and (2.29). In these cases, the linear systems produce characteristic equations combining Laplace-transforms of the convolution kernels. As a simple example of such characteristic equa-

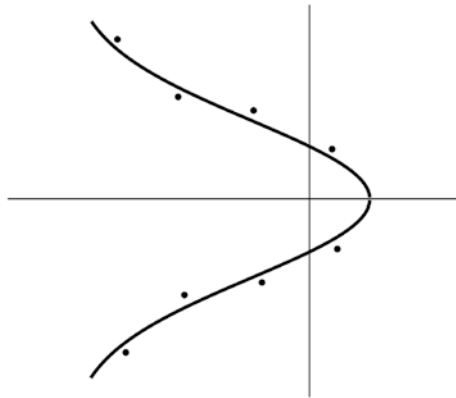


Fig. B.1 A typical location of the roots of the characteristic equation (B.6)

tions we mention (2.30), relative to (2.29), that identifies the singularities of the Laplace transform of the solution

$$\widehat{B}(\lambda) = \frac{\widehat{F}(\lambda)}{1 - \widehat{K}(\lambda)}.$$

Here, again, such singularities allow to determine the asymptotic behavior of the solution through an asymptotic expansion. Indeed this is the procedure we have applied to (2.29) in Sect. 2.5.

B.3 Non-linear delay equations, stability of steady states, bifurcations

The analysis of the linear case, discussed in the previous section, is also the basis for going through the paradigm of asymptotic stability of equilibria. Actually, in the case of equations such as (B.1) and (B.2), the search for equilibria, i. e. of constant solutions, has no special aspect and we are left with algebraic equations such as

$$F(u^*, u^*) = 0,$$

for eq. (B.1), and

$$au^* = F(u^*, u^*)$$

for (B.2), where we use (B.3). Then, linearizing (B.1) and (B.2) at u^* , for the deviation $\omega(t) = y(t) - u^*$ we get linear equations such as

$$\omega'(t) = F_x(u^*, u^*)\omega(t) + F_y(u^*, u^*)\omega(t - \tau)$$

or

$$a\omega'(t) = F_x(u^*, u^*)\omega(t) + F_y(u^*, u^*) \int_{-\infty}^t K(t-s)\omega(s) ds$$

and the respective characteristic equations

$$\lambda - F_x(u^*, u^*) - F_y(u^*, u^*)e^{\tau\lambda} = 0 \quad (\text{B.7})$$

or

$$a\lambda - F_x(u^*, u^*) - F_y(u^*, u^*)\widehat{K}(\lambda) = 0. \quad (\text{B.8})$$

Then, the paradigm of asymptotic stability is in force:

let u^* be an equilibrium of eq. (B.1) (resp. (B.2)), then, if all the roots of the characteristic equation (B.7) (resp. (B.8)) have negative real part, the equilibrium u^* is asymptotically stable; if at least one root has a positive real part it is unstable.

Here we have again a main tool for the analysis of the behavior of solutions. In particular we may explore steady states stability depending on significant param-

ters of the equation, finding bifurcation points etc ... along a theory parallel to that available for Ordinary Differential Equations, including Hopf bifurcation when a couple of complex roots cross the imaginary axis. Thus the analysis of the models can be performed through the study of characteristic equations. Actually the theory works through technicalities that go beyond our purposes, and we should not be satisfied of knowing how the roots move in the complex plane but we should verify conditions that allow to discern among different possibilities. However a complete rigorous treatment goes beyond our purposes, and we adopt a more empirical approach possibly based on numerical simulations.

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Appendix C

Discrete dynamics

Difference equations, recursive relations, discrete mathematics, . . . namely rules for building number sequences, have been on the stage for centuries, mainly to define approximating procedures, especially in connection with numerical methods. However, in more recent years, iterative procedures arose in the context of the modeling of natural phenomena, and the concept of a (time) discrete dynamical system has been developed for a parallel and alternative approach to the theory based on differential equations. In Chap. 3 we have in fact discussed several population models, embedded in the framework of a time discrete description, here we give an account of some basic facts and results that we have used in the analysis. Some of the basic references have been already quoted in Chap. 3: [2] and [5]; a more introductory presentation including Ordinary Differential Equations and Discrete Dynamical Systems is in [4] while [1] gives extended applications to ecological studies. Finally, [3] provides the basic results of the qualitative theory, while elementary and less elementary bifurcations are discussed in [6] and [7].

C.1 One dimensional dynamics

We start with the basic one-dimensional case of the discrete equation

$$x_{n+1} = F(x_n), \quad x_0 \in \mathbb{R} \quad \text{assigned}, \quad (\text{C.1})$$

where $F : \mathbb{R} \rightarrow \mathbb{R}$ is a real function that we assume to be continuously differentiable.

The graphic method describing the steps to build the sequence $\{x_n\}$ is shown in Fig. C.1. This is the *cobwebbing method* that we have used to illustrate the behavior of the models discussed in Chap. 3.

The first step in the analysis of (C.1) is, of course, the search for equilibria corresponding to constant solutions $x_n \equiv x^*$. Then we have to solve the equation

$$x = F(x)$$

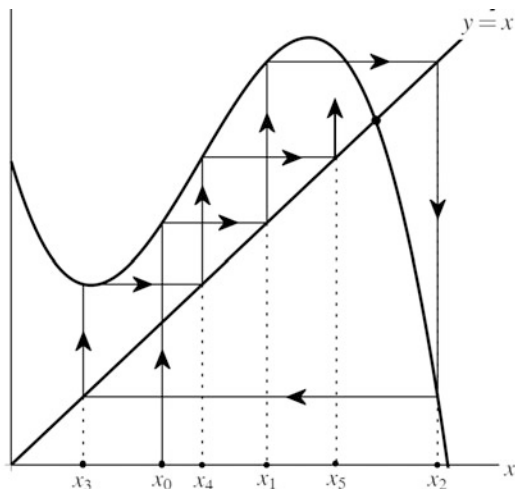


Fig. C.1 The cobwebbing method: starting from x_0 on the x -axis, x_1 is the ordinate of the point $(x_0, F(x_0))$ reached with a vertical line from x_0 ; we draw a horizontal segment from $(x_0, F(x_0))$ to the line $y = x$, in order to find x_1 on the x -axis, just drawing the vertical segment (dotted line) from the line to the axis; we can then obtain x_2 from x_1 with the same procedure, and continue onwards

i.e. we have to find the fixed points of $F(\cdot)$. In the same Fig. C.1 a fixed point is shown as the intersection of the graph of $F(\cdot)$ with the bisector line $y = x$. Stability of equilibria is defined exactly like in Sect. A.2 for differential equations, except that $n \in \mathbb{N}$ has to be substituted to $t \geq 0$.

Concerning stability of an equilibrium, the main tool is again linearization, i.e. reducing to the linear equation

$$\omega_{n+1} = F'(x^*)\omega_n$$

formulated for the deviation $\omega_n = x_n - x^*$. This linear problem has been already considered in Chap. 3 as the Malthus model. We draw the general statement

Theorem C.1. *Let x^* be an equilibrium of (C.1). Then*

- *if $|F'(x^*)| < 1$ then x^* is asymptotically stable;*
- *if $|F'(x^*)| > 1$ then x^* is unstable.*

Note that, with respect to the case of ordinary differential equations, the condition $|F'(x^*)| < 1$ replaces the negativity condition $F'(x^*) < 0$. This *correspondence principle* can be pushed farther.

In Chap. 3 we have seen how rich can be the behavior of the sequence x_n generated by $F(\cdot)$. Indeed existence of *periodic points*, i.e. of fixed points of iterates of the function

$$F^{(k)}(\cdot) = F \circ F \circ F \circ \dots \circ F(\cdot)$$

is one of the possible outcome corresponding to periodic solutions of the discrete dynamical system generated by $F(\cdot)$. The quadratic model considered in Sect. 3.1 is

a kind of prototype that can illustrate the general situation and we refer to [5] for a study in depth of this matter.

C.2 n -dimensional discrete dynamical systems

Consider the function $\mathbf{F} : \mathbb{R}^k \rightarrow \mathbb{R}^k$ and the sequence

$$\mathbf{X}_{n+1} = \mathbf{F}(\mathbf{X}_n) \quad (\text{C.2})$$

generated from a given \mathbf{X}_0 .

Within this framework, the linear case reads

$$\mathbf{X}_{n+1} = A\mathbf{X}_n \quad (\text{C.3})$$

where A is an $k \times k$ matrix. The sequence \mathbf{X}_n is then given by

$$\mathbf{X}_n = A^n \mathbf{X}_0 \quad (\text{C.4})$$

and the asymptotic behavior can be determined through the eigenvalues of A . Indeed if λ_i are the eigenvalues ($i = 1 \cdots p$), with respective multiplicity m_i ($m_1 + m_2 + \cdots + m_p = k$), then (C.4) is given by

$$\mathbf{X}_n = \sum_{i=1}^p \sum_{j=1}^{m_i-1} n^j \lambda_i^n \mathbf{v}_{ij}, \quad (\text{C.5})$$

where, for each i , the vectors \mathbf{v}_{ij} are the projection of the initial point \mathbf{X}_0 on the space spanned by the generalized eigenvectors of λ_i . As a matter of fact, we have a framework perfectly parallel to that outlined in Appendix A (Sect. A.3) for linear systems of Ordinary Differential Equations. Then, the behavior of X_n as far as stability of the origin \mathbf{O} is concerned is determined in the following theorem.

Theorem C.2. *For system (C.3) the origin \mathbf{O} is*

1. *Asymptotically stable, if and only if $|\lambda_i| < 1$ for all $i = 1, \dots, p$.*
2. *Unstable, if there exists \bar{i} such that $|\lambda_{\bar{i}}| > 1$.*
3. *Stable, if $|\lambda_i| \leq 1$ for all $i = 1, \dots, p$, and all eigenvalues with null real part are simple.*

Of course the conditions of the previous theorem can be restated in terms of the *spectral radius* of the matrix A , defined as

$$\rho(A) = \lim_{n \rightarrow +\infty} \|A^n\|^{\frac{1}{n}} = \max_{i=1, \dots, p} |\lambda_i|.$$

In fact, the three conditions of the theorem respectively correspond to

$$\rho(A) < 1, \quad \rho(A) > 1, \quad \rho(A) \leq 1.$$

Also, from (C.5) we see that, since $\rho(A)$ determines a set of leading eigenvalues, say λ_i , with $i = 1, \dots, h$, such that $|\lambda_i| = \rho(A)$, then X_n behaves asymptotically as

$$X_n \approx \rho^n(A) \sum_{i=1}^h \sum_{j=1}^{m_i-1} n^j \mathbf{v}_{ij}.$$

For planar systems we have a simple criterion to check condition 1 of Theorem C.2

Proposition C.1 (Jury condition). *For a 2×2 matrix A we have $\rho(A) < 1$ if and only if*

$$\det(A) < 1, \quad -\det(A) - 1 < \operatorname{tr}(A) < \det(A) + 1.$$

To some degree, the qualitative theory of discrete systems is parallel to what shown for differential equations in Appendix A. An equilibrium \mathbf{X}^* of system (C.2) is a solution of

$$\mathbf{F}(\mathbf{X}^*) = \mathbf{X}^* \quad (\text{C.6})$$

Concerning its stability, the following linearization theorem, analogous to Theorem A.9, holds

Theorem C.3. *Let \mathbf{X}^* be an equilibrium of system (C.2), and let $A = \mathbf{JF}(\mathbf{X}^*)$ the Jacobian of \mathbf{F} at \mathbf{X}^**

- *if $\rho(A) < 1$, \mathbf{X}^* is asymptotically stable;*
- *if $\rho(A) > 1$, \mathbf{X}^* is unstable.*

We do not go into further details of the qualitative theory of the difference equation (C.2), as in our analysis of the discrete models of Chap. 4 we have used only very basic results of this theory. It is instead worthwhile giving a sketch of the simplest equilibrium bifurcations of discrete systems, stressing the similarities with what presented in Sect. A.10 as well as the new phenomena.

C.3 Bifurcations

Consider a family of difference equations depending on a parameter α (in \mathbb{R})

$$\mathbf{X}_{n+1} = \mathbf{F}(\alpha, \mathbf{X}_n) \quad (\text{C.7})$$

where $\mathbf{X}_n \in \mathbb{R}^n$, and $\mathbf{F}(\cdot, \cdot)$ is regular enough (we do not go in details here). The equilibria will be denoted as \mathbf{X}_α depending on α ; the corresponding Jacobian matrix $\mathbf{J}(\alpha) = \mathbf{JF}(\alpha, \mathbf{Y}_\alpha)$. According to Theorem C.3, changes in the stability occur only when one eigenvalue of $\mathbf{J}(\alpha)$ crosses the circle $|\lambda| = 1$,

Then we consider four types of elementary bifurcations:

- **tangent bifurcation** $\mathbf{J}(\alpha^*)$ has eigenvalue 1 and $\mathbf{F}_\alpha(\alpha^*, \mathbf{Y}_{\alpha^*}) \neq 0$;
- **transcritical bifurcation** $\mathbf{J}(\alpha^*)$ has eigenvalue 1 but $\mathbf{F}_\alpha(\alpha^*, \mathbf{Y}_{\alpha^*}) = 0$;

- **Neimark-Sacker (Hopf) bifurcation** $\mathbf{J}(\alpha^*)$ has eigenvalues $a \pm i\omega$ (with $a^2 + \omega^2 = 1$ and $\omega > 0$);
- **period-doubling bifurcation** $\mathbf{J}(\alpha^*)$ has eigenvalue -1

The first two types are completely analogous to the case of differential equations, and are not explicitly discussed, while Neimark-Sacker bifurcation differs somewhat from Hopf bifurcation for differential equations. Finally, period-doubling bifurcation is an equilibrium bifurcation specific to difference equations.

Neimark-Sacker bifurcation

A prototype system is

$$\begin{cases} x_{n+1} = (\alpha \pm (x_n^2 + y_n^2))(x_n \cos(\varphi) - y_n \sin(\varphi)) \\ y_{n+1} = (\alpha \pm (x_n^2 + y_n^2))(x_n \sin(\varphi) + y_n \cos(\varphi)) \end{cases} \quad (\text{C.8})$$

with $\varphi \neq 0, \pi$. The origin $(0, 0)$ is an equilibrium of (C.8) for all values of α and its Jacobian is

$$J(\alpha) = \begin{pmatrix} \alpha \cos(\varphi) & -\alpha \sin(\varphi) \\ \alpha \sin(\varphi) & \alpha \cos(\varphi) \end{pmatrix}$$

whose eigenvalues are $\lambda_{\pm} = \alpha(\cos(\varphi) \pm i \sin(\varphi))$.

Hence $(0, 0)$ is asymptotically stable for $|\alpha| < 1$ and unstable for $|\alpha| > 1$ with two complex-conjugate eigenvalues crossing $|\lambda| = 1$ at $\alpha = 1$ (and also at $\alpha = -1$). To understand the global behavior, (C.8) can be written in polar coordinates, yielding

$$\begin{cases} \rho_{n+1} = (\alpha \pm \rho_n^2)\rho_n \\ \vartheta_{n+1} = \vartheta_n + \varphi. \end{cases} \quad (\text{C.9})$$

Again we can distinguish a supercritical bifurcation (when there is a $-$ sign in front of ρ_n^2) from a subcritical bifurcation (when there is a $+$ sign). In the former case, the circle $\rho = \sqrt{\alpha - 1}$ is invariant for system (C.9) when $\alpha > 1$ and attractive, as can be seen by looking at the first of (C.9) as a one-dimensional discrete system. The solutions of (C.9) move along that circle with a constant shift of an angle φ . If φ and π are commensurable, $\vartheta_n = \vartheta_0$ for some n and solutions on the circle are periodic. Otherwise, solutions are aperiodic, but quasi-periodic.

In the case of a subcritical bifurcation, the circle $\rho = \sqrt{1 - \alpha}$ is invariant and repulsive for $0 < \alpha < 1$. Again, solutions on the circle may be periodic (if φ and π are commensurable) or quasi-periodic, otherwise.

Without going into details that can be rather complex (see, e.g. [6]), for a generic map for which, moving from $\alpha < \alpha^*$ to $\alpha > \alpha^*$, an equilibrium \mathbf{X}_{α} becomes unstable through two complex-conjugate eigenvalues crossing $|\lambda| = 1$ at $\alpha = \alpha^*$, a closed invariant curve emerges from the equilibrium \mathbf{X}_{α} , either for $\alpha > \alpha^*$ (supercritical case) or for $\alpha < \alpha^*$. Along the closed invariant curve, solutions may be periodic, or quasi-periodic.

Period-doubling (or flip) bifurcation

The last instance concerns what happens when an eigenvalue of the Jacobian crosses the unit circle at $\lambda = -1$. An example of this type can be seen for the discrete logistic map in Sect. 3.1.

We illustrate this case by the recurrence

$$x_{n+1} = F(x_n) \quad \text{with} \quad F(x) = -(1 + \alpha)x \pm x^3. \quad (\text{C.10})$$

It is clear that 0 is an equilibrium for all α and there are no other equilibria in a neighborhood; furthermore, the equilibrium changes from asymptotically stable to unstable at $\alpha = 0$ through its Jacobian being equal to -1 at $\alpha = 0$.

Let us consider first the (supercritical) case with the sign $+$ in the function F . Then its iterate

$$F^{(2)}(x) = x(x^2 - (1 + \alpha)) [x^2(x^2 - (1 + \alpha))^2 - (1 + \alpha)]$$

has as fixed points, beyond $x = 0$, also $x_{1,2} = \pm\sqrt{\alpha}$ for $\alpha > 0$. $x_{1,2}$ are not fixed points of F , thus they are not equilibria of (C.10), but constitute a 2-periodic solution: $x_2 = F(x_1)$ and $x_1 = F(x_2)$.

Furthermore, by examining, for instance by the cobwebbing method, the discrete dynamical system $x_{n+2} = F^{(2)}(x_n)$, one sees that the 2-periodic solution is attracting. Summarizing, the 0 equilibrium is attracting for $\alpha < 0$ (and > -2), and repulsive for $\alpha > 0$. For $\alpha > 0$, the 2-periodic solution (x_1, x_2) emerges from the equilibrium and is attracting.

When there is a sign $-$ in the function F , one has a subcritical bifurcation. Precisely one obtains

$$F^{(2)}(x) = x(x^2 + (1 + \alpha)) [x^2(x^2 + (1 + \alpha))^2 + (1 + \alpha)]$$

and one can check that $x_{1,2} = \pm\sqrt{-\alpha}$ are fixed point of $F^{(2)}$ when $\alpha < 0$. Furthermore, the resulting 2-periodic solution of (C.10) is repulsive.

The general case of an equilibrium \mathbf{X}_α becoming unstable at $\alpha = \alpha^*$ through an eigenvalue $\lambda = -1$ is analogous, under some technical conditions. A 2-periodic solution emerges from the equilibrium \mathbf{X}_{α^*} , either for $\alpha > \alpha^*$ (when \mathbf{X}_α is unstable) and is then attracting (supercritical case), or for $\alpha < \alpha^*$ (when \mathbf{X}_α is asymptotically stable) and is then repulsive (subcritical case).

C.4 Bifurcations of periodic solutions of ODE

Stability and bifurcations of periodic solutions of autonomous ordinary differential equations can be reduced to the study of equilibrium bifurcations of discrete systems through the tool of Poincaré maps. Without going into technical details (see,

e.g., [7]), taken a point \mathbf{Y}^* on a periodic orbit of the differential equation

$$\mathbf{Y}'(t) = \mathbf{F}(\mathbf{Y}(t)) \quad (\text{C.11})$$

and an $(n-1)$ -hyperplane H transverse to the orbit through \mathbf{Y}^* , one can define a map P that, for each point $\mathbf{Y} \in H$ close to \mathbf{Y}^* , returns the point $P(\mathbf{y})$ where $\mathbf{Y}(\cdot, \mathbf{Y})$, the solution of (A.20) starting from \mathbf{Y} , first returns to H .

Clearly \mathbf{Y}^* is a fixed point of the map P , and it is not difficult to see that the periodic solution is attracting (resp. repulsive) if and only if \mathbf{Y}^* is attracting (resp. repulsive) as an equilibrium of the discrete system $\mathbf{Y}_{n+1} = P(\mathbf{Y}_n)$. The conditions correspond to what discussed in Appendix A about Floquet multipliers.

This reduction makes us understand that to each equilibrium bifurcation of discrete systems, a corresponding bifurcation of periodic orbits exists. One can then have:

- **tangent bifurcation:** two periodic orbits exist for $\alpha > \alpha^*$ and merge at α^* in a single orbit \mathcal{P}_{α^*} , while no periodic orbits exist for $\alpha < \alpha^*$ in a neighborhood of \mathcal{P}_{α^*} . For $\alpha > \alpha^*$, the dimension of the stable manifold differs of 1 between the two periodic orbits (in particular one of them may be attracting, while the other is certainly unstable);
- **transcritical bifurcation:** two branches of periodic orbits cross at $\alpha = \alpha^*$, and exchange dimension of their stable manifolds (in particular one branch is attracting for $\alpha < \alpha^*$, the other one for $\alpha > \alpha^*$);
- **period doubling bifurcation:** a branch of periodic orbits \mathcal{P}_α becomes unstable at $\alpha = \alpha^*$ through an eigenvalue of the Jacobian its Poincaré map being -1 (more generally, one can consider the case where one eigenvalue, not necessarily the leading one is equal to -1); then another branch of periodic solutions emerges from the previous one at \mathcal{P}_{α^*} of period approximately twice as long. This branch exists either for $\alpha > \alpha^*$ (when \mathcal{P}_α is unstable) and is then attracting (supercritical case), or for $\alpha < \alpha^*$ (when \mathcal{P}_α is asymptotically stable) and is then repulsive (subcritical case). For reasons related to Poincaré-Bendixson theory, this type of bifurcation can occur only if $n \geq 3$;
- **torus bifurcation:** it occurs when a branch of periodic orbits \mathcal{P}_α becomes unstable at $\alpha = \alpha^*$ through two complex conjugate eigenvalues of the Jacobian its Poincaré map crossing the circle $|\lambda| = 1$. Thus, it occurs when the Poincaré map undergoes a Neimark-Sacker bifurcation. The closed invariant curve for the Poincaré map becomes a torus-like invariant surface for (A.20), over which solutions may be periodic or quasi-periodic. This type of bifurcation, here described in its simplest form, can clearly occur only when the Poincaré map is at least 2-dimensional, so for $n \geq 3$.

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Appendix D

Continuous-time Markov chains

We present here a short summary of the parts of the theory of Markov processes with countable state space that is used in the chapters describing stochastic models of populations. The presentation will be restricted to Markov process that are generated by an infinitesimal transition matrix, as discussed below.

This treatment is inspired in particular to the books by Karlin and Taylor [4], to which we refer for many extensions. A rigorous, but still relatively simple, treatment can be found in [3], from which we took some statements, and to which we refer for further details.

The general theory of Markov processes with countable state space is presented concisely and clearly by Liggett [2] and with more details by Anderson [1].

D.1 Markov processes

A Markov process with countable state space E is a stochastic process $X(t)$, $t \geq 0$ that takes values in E (E can be identified with \mathbb{N} , when it is actually countable, or with $\{0, 1, \dots, n\}$ when it is finite) and satisfies the Markov property

$$\mathbb{P}(X(t) = j | X(s_1) = i_1, X(s_2) = i_2, \dots, X(s_n) = i_n, X(s) = i) = \mathbb{P}(X(t) = j | X(s) = i)$$

for all choices of $0 \leq s_1 < s_2 < \dots < s_n < s < t$, $j, i, i_1, \dots, i_n \in E$.

We further require that all trajectories are continuous from the right (this assumption ensures that events like $\{X_t = i \text{ for some } t > 0\}$ are measurable) and that the transitions probabilities are stationary, i.e.

$$\mathbb{P}(X(t) = j | X(s) = i) = \mathbb{P}(X(t-s) = j | X(0) = i) := P_{ij}(t-s)$$

$\forall 0 \leq s < t$, $i, j \in E$.

The functions $P_{ij}(t)$ are called the transition functions of the process, and can be written as an (infinite) matrix. They have the following properties (rather obvious

from simple probability arguments):

- i) $P_{ij}(t) \geq 0$ and $P_{ij}(0) = \delta_{ij}$ for all $i, j \in E$,
- ii) $\sum_{j \in E} P_{ij}(t) = 1$ for all $i \in E, t \geq 0$,
- iii) $P_{ij}(t+s) = \sum_{k \in E} P_{ik}(t)P_{kj}(s)$ for all $i, j \in E, t, s \geq 0$.

The equations at point iii) are named *Chapman-Kolmogorov equations*: intuitively they say that for going from i in j in time $t+s$, the process will move to some k in time t , and then from k to j in time s .

From the transition functions $P_{ij}(t)$, one can compute $\mathbb{P}(X(t) = j)$ for all j , once the initial conditions are assigned. Indeed, if we set $\mathbb{P}(X(0) = i) = \pi_i$ where $\{\pi_i, i \in E\}$ is a probability distribution, then

$$\mathbb{P}(X(t) = j) = \sum_{i \in E} \pi_i P_{ij}(t).$$

We will consider only transition functions (called standard) that satisfy also the property

- iv) $\lim_{t \rightarrow 0} P_{ii}(t) = 1$ for all $i \in E$; it follows $\lim_{t \rightarrow 0} P_{ij}(t) = \delta_{ij}$ for all $i, j \in E$.

From these properties, it can be proved that the transition function must be differentiable. Precisely:

Proposition D.1. *For all $i \in E$, it exists*

$$\lim_{t \rightarrow 0} \frac{1 - P_{ii}(t)}{t} := q_i.$$

It is possible that $q_i = +\infty$ in which case state i is said to be instantaneous. Otherwise, the following can also be proved

Proposition D.2. *If $q_i < +\infty$ for all $i \in E$, then there exists $q_{ij} = P'_{ij}(0)$ and is finite for all $i, j \in E$. Furthermore*

$$\sum_{j \in E} q_{ij} \leq 0, \text{ for all } i \in E.$$

The (infinite) matrix Q whose components are q_{ij} is called the *infinitesimal transition matrix* of the process $X(t)$. Note that $q_{ii} = -q_i \leq 0$, while $q_{ij} \geq 0$ for $i \neq j$.

The coefficients q_{ij} are the derivatives of $P_{ij}(t)$ at $t = 0$. There are two systems of equations, the Kolmogorov backward and forward equations, involving $P_{ij}(t)$ at all $t \geq 0$. Precisely

Proposition D.3. *If $q_i < +\infty$ and $\sum_{j \in E} q_{ij} = 0$, we have*

$$P'_{ij}(t) = \sum_{k \in E} q_{ik} P_{kj}(t) \quad i, j \in E. \quad (\text{D.1})$$

Equation (D.1) can be seen, for each j (that can be considered as a parameter), as a (finite or infinite) system of equations in the unknowns P_{ij} , $i \in E$. Formally it can be written in matrix notation as $P'(t) = QP(t)$.

In an analogous way to the backward equation, one can derive a different system of equations, known as Kolmogorov forward equations:

$$P'_{ij}(t) = \sum_{k \in E} P_{ik}(t)q_{kj} \quad i, j \in E. \quad (\text{D.2})$$

or, in matrix notation, $P'(t) = P(t)Q$. Now i can be taken as a parameter and the unknowns are P_{ij} , $j \in E$.

However, at this level of generality, it is not possible to prove that (D.2) actually holds.

D.2 Holding times and the jump Markov chain

So far, we started from a stationary Markov process, introduced the transition probability matrix $P(t)$ and, under some additional assumptions, obtained the infinitesimal transition matrix $Q(t)$ and stated that the (backward) Kolmogorov equations hold.

In applications, one generally starts from a matrix Q of infinitesimal transition. Indeed, for $i \neq j$,

$$Q_{ij} = \lim_{h \rightarrow 0^+} \frac{P_{ij}(h)}{h}$$

which can also be written as

$$P_{ij}(h) = Q_{ij}h + o(h) \quad \text{as } h \rightarrow 0^+.$$

Thus Q_{ij} represents the rate at which the system moves from state i to state j , and this is what is generally prescribed by models.

In particular, *birth-and-death processes* are Markov processes on \mathbb{N} such that $q_{i,j} = 0$ if $|i - j| > 1$. Generally, one names $\lambda_i = q_{i,i+1}$ and $\mu_i = q_{i,i-1}$.

Because of Prop. D.2, it is required that $\sum_{j \neq i} q_{ij} < +\infty$, and then one sets

$$q_i = \sum_{j \neq i} q_{ij}, \quad q_{ii} = -q_i$$

so that necessarily

$$q_i < +\infty \text{ and } \sum_{j \in E} q_{ij} = 0.$$

From the matrix Q , a constructive procedure shows that there exists a Markov process with transition probability $P(t)$ that has Q as infinitesimal transition matrix and satisfies backward and forward Kolmogorov equations. In general, there may be other Markov processes having Q as infinitesimal transition matrix; a hint is given in a special case.

The constructive procedure is based on the following ideas. Let $X(t)$ be a Markov process with countable state space and right-continuous trajectories, and

$$\tau = \inf\{t > 0 : X(t) \neq X(0)\}.$$

Then, if $q_i > 0$,

$$\mathbb{P}(\tau > t | X(0) = i) = e^{-q_i t} \quad \text{and} \quad \mathbb{P}(X(\tau) = j | X(0) = i) = \frac{q_{ij}}{\sum_{k \neq i} q_{ik}}.$$

If $q_i = 0$, $X(t) \equiv i$ for all $t > 0$ with probability 1, and i is defined an *absorbing state*.

Because of the Markov property (and the stationarity), $X(t)$ will continue for $t > \tau$. We will then have a sequence of jump times with holding times exponentially distributed in between; the transition probabilities at jump times will be given by

$$\frac{q_{ij}}{\sum_{k \neq i} q_{ik}}.$$

Let then

$$\rho_{ij} = \begin{cases} \frac{q_{ij}}{\sum_{k \neq i} q_{ik}} & \text{if } q_i > 0 \text{ and } j \neq i \\ 0 & \text{if } q_i > 0 \text{ and } j = i \\ 1 & \text{if } q_i = 0 \text{ and } j = i \\ 0 & \text{if } q_i = 0 \text{ and } j \neq i \end{cases}$$

and define Z_n , $n \geq 0$ as a Markov chain with transition probabilities ρ (the *jump Markov chain* embedded in $X(t)$) and with initial distribution of Z_0 equal to π .

Let T_n , $n \geq 1$ a sequence of exponential (of parameter 1) random variables independent of each other and of the Markov chain Z_n ; let then $\tau_n = T_n / q_{Z_{n-1}}$ and $J_n = \sum_{k=1}^n \tau_k$ with $J_0 = 0$. Notice that τ_n will be exponential random variables of parameter $q_{Z_{n-1}}$, and J_n will represent the jump times of the process.

Finally define

$$X(t) = Z_n \quad \text{if } J_n \leq t < J_{n+1}. \quad (\text{D.3})$$

It is not difficult to show that $X(t)$ defined in this way is a right-continuous Markov process having Q as infinitesimal transition matrix and π a distribution of $X(0)$. Furthermore, it is possible to show that its transition probabilities $P(t)$ satisfy both backward and forward Kolmogorov equations.

A problem in the previous construction arises if $\sum_{n=1}^{\infty} \tau_n < +\infty$. Then $\lim_{n \rightarrow \infty} J_n = J_{\infty} < +\infty$ and the process $X(t)$ is not defined for $t \geq J_{\infty}$.

Building instances in which this actually happens is easy. Takes for instance a pure birth process, i.e. a birth-and-death process with $\mu_i \equiv 0$, where $\lambda_i = i^2$, and $X(0) = 1$.

The Markov chain Z_n will be deterministic, since transitions can only be upwards, with $Z_n = n + 1$. Then τ_n are exponential random variables of parameter n^2 so that

$\mathbb{E}(\tau_n) = 1/n^2$. Hence

$$\mathbb{E}\left(\sum_{n=1}^{\infty} \tau_n\right) = \sum_{n=1}^{\infty} \frac{1}{n^2} < +\infty \implies \sum_{n=1}^{\infty} \tau_n < +\infty \quad \text{w.p. 1.}$$

Note that this is the same phenomenon occurring in differential equations. If one takes the differential equation corresponding to this birth process $N'(t) = N(t)^2$, $N(0) = 1$, it is well known that the solution is $N(t) = (1 - t)^{-1}$ which is defined only for $t < 1$: there is no global solution to the equation, since the solution reaches infinite in finite time (*explosion* in finite time).

The previous procedure leaves undefined the process for $t \geq J_\infty$; in this way, we would obtain defective transition probabilities, i.e. $\sum_{j \in E} P_{ij}(t) < 1$. It is possible to build Markov processes that coincide with this one for $t < J_\infty$ and are then extended in different ways: for instance, we could set $X(J_\infty) = 1$ and let the process continue with the same rules. In this sense, the previous procedure builds the minimal process generated by the infinitesimal transitional matrix Q .

From the modeling point of view, we can view these as mathematical pathologies that should be avoided through appropriate assumptions. For instance, for birth-and-death processes, an assumption that avoids this type of “explosion in finite time” is

$$\lambda_i \leq a + bi, \quad i \in \mathbb{N}$$

where a and b are nonnegative constants. Under such an assumption, there exists a unique process $X(t)$ which is generated by $Q(t)$, and can be obtained with the above construction as $J_\infty = +\infty$ w.p. 1.

D.3 Stationary distributions

An interesting question for all Markov processes is whether there exists a stationary distribution. In words, a stationary distribution has the property that, if the process follows the stationary distribution at time $t = 0$, it will follow the same distribution at any time $t > 0$. Thus, a stationary distribution can be seen as corresponding to an equilibrium of a deterministic system. In formula, we say that $\{\pi_i, i \in E\}$ is a stationary distribution if

$$\sum_{i \in E} \pi_i P_{ij}(t) = \pi_j, \quad \text{for each } j \in E, t > 0. \quad (\text{D.4})$$

If i is an absorbing state, the Dirac distribution centered in i ($\delta_i = 1$, $\delta_j = 0$ if $j \neq i$) is clearly a stationary distribution, but not a very interesting one.

We then look for stationary distributions in chains without absorbing states and with a single communicating class, i.e. for all i and $j \in E$, there exists t such that $P_{ij}(t) > 0$. In these cases, the following result states a dichotomy for existence of a stationary distribution, and also says that stationary distributions are attractive.

Theorem D.1 (Theorem 5.1.6 in [1]). *If there exists a unique communicating class, then*

$$\lim_{t \rightarrow \infty} P_{ij}(t) = u_j \text{ exists and does not depend on } i.$$

Either $u_j \equiv 0$ or $u_j > 0$ for all $j \in E$; in the latter case, u_j is a stationary distribution.

Vice versa, if w is a stationary distribution, then $\lim_{t \rightarrow \infty} P_{ij}(t) = w_j$ for all i .

Note that if the state space is finite, it is not possible that $u_j \equiv 0$; hence, a stationary distribution necessarily exists.

Comparing this result with the corresponding results for discrete-time Markov chains, it can be noticed that this result is simpler, as it is not necessary to ask for aperiodicity of the chain.

Definition (D.4) is not very amenable to a direct check, because the condition has to be satisfied at every $t > 0$ and $P_{ij}(t)$ are generally not known explicitly.

On the other hand, taking the derivative of (D.4) with respect to t , computing it in $t = 0$ and remembering that $P'_{ij}(0) = q_{ij}$, one obtains

$$\sum_{i \in E} \pi_i q_{ij} = 0 \quad \forall j \in E. \quad (\text{D.5})$$

It is not difficult to prove [1, Thm. 5.4.3] that (D.5) is necessary and sufficient for $\{\pi_i, i \in E\}$ to be a stationary distribution, when all $\pi_i > 0$ and the Markov process is the one obtained by the construction in Sect. D.2.

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