Ivan Maly

Quantitative Elements of General Biology

A Dynamical Systems Approach

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Contents

Abbreviations

cAMP	Cyclic adenosine monophosphate
CAP	Catabolite activator protein
EGF	Epidermal growth factor
EGFR	Epidermal growth factor receptor
FGF	Fibroblast growth factor
MAPK	Mitogen-activated protein kinase
MAPKK	Mitogen-activated protein kinase kinase
MAPKKK	Mitogen-activated protein kinase kinase kinase
RTN	Retrotrapezoid nucleus
WASP	Wiskott-Aldrich syndrome protein

Chapter 1
Introduction

As a field of study, general biology seeks to identify dynamic processes and functional structures that are common to all life forms. Owing to the extreme diversity of living organisms, the goal of general biology can also include identification of what is sufficiently widespread among life forms, and explanation of the mechanistic reasons for the variation. General biology is therefore related in its methodology to comparative biology, although the emphasis is on commonality and not the differences. Toward this aim, general biology integrates the results of disciplines such as cell biology, physiology, ecology, and others, insofar as they are not specific to the taxa studied. The range of topics covered by general biology acquired its present breadth by the time when the fundamental findings in molecular biology became fully systematized. These topics include (see Libbert 1982) the distinction of living from non-living matter, metabolism, genetics, mechanisms of proliferation, embryology, control mechanisms, behavior, evolution, and ecological interactions. In addition to a dramatic progress that has been achieved in many of these areas with the application of novel methods in recent years, a new emphasis on system-level properties that are common to different taxa has emerged (see, *e.g.*, Alon 2006; Maly 2008; Klipp et al. 2009; Prokop and Csukas 2013; Rajewsky et al. 2018).

The quantitative approach has been indispensable to advancement of general biology. Beginning with the example of Mendel, development of statistics was intertwined with the progress in genetic research (see, for example, Fisher 1999), a process that continues with today's machine learning and genomics. To take an obvious and well-studied example, whether one, two, three, or four leaves are formed at a time during the growth of a plant shoot is a quantitative question that we are to have a systematic answer for if general understanding of plant habits is the goal. However, development of self-organization science in the twentieth century (*e.g.*, Haken 1983) has shown that the more fundamental problem of why a defined number of discrete organs (leaves) is formed in such cases, instead of a random number of them or, say, a continuous collar of light-capturing tissue, is also a problem to be answered through application of quantitative methods. In this example as

in many others of its nature, the emergence of the biologically functional pattern is a quantitative effect arising in a system of interacting elements (cells, molecules) and cannot be explained—whether qualitatively or with precision—other than as a property of the dynamics of the system components' interaction. Although application of the methods of dynamical systems research to biology has a considerable pedigree (see, *e.g.*, Rosen 1970) and has impacted the development of the mathematical methods themselves (Tu 1994; Jost 2005), the recent emphasis on systems explanations in biological science has led to a solidification of the dynamical systems approach (*e.g.*, Murray 2002; Garfinkel et al. 2017; Chen and Zaikin 2021).

The quest for identification of processes general to all life has suffered from a problem threatening to reduce all answers to something very near tautology: since reproduction and inheritance are attributes that unquestionably belong to the definition of life, and we accept all life—whether extant or known from the paleontological record—to have common ancestry, any features identified as common may simply be inherited. Indeed, this could be so whether these features be deterministically attached to all life or merely accidents of life's origin and early evolution. While this problem may not be fully resolved for some time, advances in astrobiology and particularly in methods of detection and future study of life on other planets (Yamagishi et al. 2019) are beginning to supply hope that juxtaposition of life as we know it with independent, or at least widely separated life forms may become possible. Such comparison would be uniquely informative for general biology, as it would enable separating the accidental, masquerading as universal, from what is truly universal among the properties of living matter.

For general biology, therefore, this is the time to systematize our understanding from the perspective of identifying, among the features common to life as we know it, those that are likely generalizable beyond the singular example we have been studying. Even if at present this may appear to be an exercise in hypothesis-making, demand for a well-grounded set of generalizable life attributes can become acute very soon with the accelerating pace of developments in astrobiology. As regards the generalizable planetographic conditions for life's emergence and existence, as well as planetographic signatures of extant life, this direction of study is comparatively advanced (Yamagishi et al. 2019). What will be required following a definitive discovery of extraterrestrial life—which we expect to come in the form of discovery of its planetographic signature—will be guidance from general biology with respect to the dynamic and structural features of such life that may be rationally expected, based on our experience with studying life terrestrial, so that more detailed data could be efficiently collected and interpreted.

General biology, now understood more narrowly as generalizable biology in the above sense, can, in principle, encompass a very wide range of life attributes. For example, requirements concerning the chemical composition of living matter may be addressed. Not even a review of possible directions in such a broad, interdisciplinary study will be attempted here. Instead, our subject will be confined to sketching out a set of dynamical attributes that is identifiable with life and can be expected

to be generalizable from life as we know it to its possibly unrelated forms that may be discovered in the future.[1]

Having considered the old and new motivation for identifying the general (*i.e.*, generalizable) dynamical systems properties and processes that are associated with living matter, how can we approach this problem on our present level of understanding and in a format that is both writable and readable? A compendium (the word from the title of the first work cited in this chapter, a classic of non-mathematical general biology) of dynamical systems results pertinent to generalizable biology is not feasible at this point, before the overall direction has been sketched out, debated, and accepted. What follows, therefore, is of necessity an incomplete and somewhat subjective version of such a sketch, but one that is intended to serve the modest purpose just stated.

When selecting the topics to cover and their sequence, we need to be mindful of the problem of circularity in all biological reasoning, which stems from the already mentioned issue of the subject of our study arising from self-replication. A process may be mechanistically fundamental with respect to another process, yet its very existence may be contingent on the higher-level process and its kinetics controlled by the latter through evolutionary dynamics, whereby fundamental processes are fine-tuned to answer the needs of the higher-level ones. Today's didactic literature covering general biology comports with the paradigm of the cited twentieth-century compendium and usually adopts the mechanistic logic, proceeding from the molecular basis of life, through physiology, to ecology and biogeography. Here, we will take a slightly different approach. Processes responsible for the very existence of living matter in defined forms will be considered first (ecologically abstracted biomass growth kinetics, followed by elementary speciation and homeostasis). From there on, our sequence will be more conventional, covering elements of cell biology, multicellular development, ecology, ending in treatment of evolution from the standpoint of species interaction. A degree of circularity in the exposition, whereby the most elementary ecology and evolution is considered first, and more complex effects in the same realms last, should be seen as intentionally reflecting the mentioned circularity in the subject matter. With this caveat, the exposition is from the elementary to the complex, and from the foundational to the mechanistically derivative.

An additional reason—besides its being fundamental to the very existence of living matter—to consider biomass growth first is that useful formalisms exist in this area of study that are both simple and illustrative of the basic concepts of biological kinetics and analysis of systems behavior. Indeed, by introducing these on the example of elementary, single-species biomass kinetics, we remain in the mold of the didactic tradition exemplified by the cited work of Murray. The need for such an opening chapter arises from our desire to make this monograph accessible also to those readers who may be less familiar with the language of dynamical systems

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[1] Since this was written, a possible phosphine biosignature has been discovered on Venus and an expedition for sample collection and study in situ has been proposed (Greaves et al. 2020).

theory. In addition to covering its biological subject, the biomass kinetics chapter (Chap. 2) can serve as a technical introduction to the quantitative approach that is followed in the rest of the book. Both continuous-time models and models with generations will be considered, the former introducing the concepts of steady states and stability analysis, and the latter, emergence of oscillations, multiperiodicity, and apparent chaos.

The jump to speciation in the third chapter may be unexpected, yet existence of species is fundamental to any quantitative treatment of organismal mechanisms and therefore precedes them in our exposition. The concept of species as defined forms that living matter can take supplies the basis for having well-defined parameter values in any model. All subsequent material in the book relies on existence of a mechanistic structure and a set of biophysical parameters that are representative of some identifiable quantity of living matter. This is possible only when the living matter is subdivided into at least tolerably delineated varieties. With this in mind, we will consider (Chap. 3) the most elementary processes in evolution, which can lead to emergence and maintenance of species. The basic results of quasi-species theory of mutation-selection balance will be laid out, followed by analysis of neutral sympatric speciation in a spatially well-mixed population.

Equally foundational to existence of all living matter are control processes that can maintain the internal environment of organisms in the variable external environment. Physiological adaptation to changing external conditions also belongs to this category of processes, as are the capabilities of organisms and cells to effect transitions between distinct physiological states when survival requires it. On the organism as well as cell level, processing of external signals is intertwined with the control processes, and the processing and control functionalities often share the same molecular substrate and rely on closely related types of nonlinear dynamics. In view of this, selected elementary examples of signal processing and functional control will be treated together in Chap. 4, to include all-or-nothing response, oscillatory control, and kinetic switches on the genetic, biochemical, cellular, and organism level.

The functional structure of the cell is the central biological element that connects life's molecular building blocks with the organismal structure and function. Owing to this, two chapters will be devoted to general biology problems that concern dynamical origins of the cell structure. In the first one (Chap. 5), we will deal with molecular self-organization in the cell. An important aspect of these processes that distinguishes them from molecular self-organization that may take place outside the biological realm is the orchestration of the molecular processes by the constraints imposed by the heritable cell structure (Harold 2001). How the large-scale structure is shaped by the kinetics of interaction of its molecular components will be addressed through the prism of quantitative models of cytoskeleton dynamics, cytoskeleton-directed and -driven motility, and spatially distributed cell signaling. Selected approaches to the fundamental problems of centered organization of advanced (eukaryotic) cells, orientational order of their cytoskeletal filaments, and overall polarity (directionality) of the cell structure will be highlighted. In Chap. 6, we will transition to treatment of system-level effects arising from mechanical forces that

are inherent in the elementary cell structure and that shape this structure further. Here—in the belief that, like the cellularity itself, the basic cytoskeletal organization should be generalizable from the known advanced life forms—the focus will be on the microtubule cytoskeleton, whose mechanics will be analyzed in the situations of isolated interphase cells, cell division, and cell-cell interactions.

The mechanisms responsible for generation of the body plan of advanced organisms have long been recognized among the central problems in general biology. The problem of multicellular morphogenesis motivated Turing in was to become one of the pivotal achievements of the twentieth century science: demonstrating a mechanism for emergence of stable spatial patterns in an initially homogeneous molecular system (Turing 1952). In Chap. 7, we will examine multicellular morphogenesis on two examples, phyllotaxis and segmentation. Phyllotaxis—developmental arrangement of leaves and other organs of vascular plants—is an example of morphogenesis that is in evidence in the world around us. Although its mechanistic substrate is widely different, as a process whereby morphological elements of the organism are produced repeatedly and regularly, phyllotaxis can be seen as related closely to segmentation in animal body plans. Outlines of our current understanding of the two comparatively complex and well-studied processes will serve to illustrate dynamical systems principles that may be broadly operational in multicellular morphogenesis.

Having sketched out the selected elements of general biology from the molecular processes to the multicellular organism form, in Chap. 8 we return to the foundational biological processes of biomass growth kinetics and evolution to reconsider them on the level of species interaction. The focus this time will be on accounting explicitly for the ecological relationships (*e.g.*, predator-prey, mutualism, or competition) as they influence the species' population dynamics and evolutionary trajectory. The ecological factors have temporal, spatial, and genome-space aspects, and may lead to self-organization in each of the three domains. The biomass dynamics considered here will be a multi-species generalization of the elementary kinetic laws from Chap. 2, and the ecological dynamics in the genotype space, derivative from the elementary formalizations for speciation given in Chap. 3. The oscillatory temporal pattern that can arise in a simple ecological model of Lotka and Volterra will be considered fist. In the remainder of the chapter, more complex, and apparently aperiodic, temporal pattern of punctuated equilibrium in an explicitly genetic model of ecological coevolution will be analyzed, followed by a discussion of spatial dynamics associated with various ecological relationships and speciation in spatially distributed populations.

The breadth of the presented topics demonstrates unity of dynamical laws and analytical approaches across several levels of biological organization, which has been attained through recent research in the different fields. While much work remains to be done to explicitly unify biological theory on the basis of the mathematical apparatus of dynamical systems, the very rough sketch of such an encompassing theory that is offered here may serve as an additional impetus for such future effort.

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Chapter 2
Biomass Growth and the Language of Dynamic Systems

2.1 Equilibria, Stability, and Hysteresis

Dynamics of biomass growth is fundamental to the very existence of living matter. Its models (see, e.g., Hastings 2000; Kot 2001) also allow us to introduce the basic concepts of biological kinetics and analysis of systems behavior on mathematically simple examples (e.g., Edelstein-Keshet 1988; Murray 2002; Riznichenko 2011). Consider the description of the biomass of a certain population with a single variable, x. A series of instructive cases can be captured by a general form in which the rate of change with time t is a polynomial in x that extends only to the third power.

The simplest case is

$$\frac{dx}{dt} = \left(k_g - k_d\right)x,$$

(2.1)

where k_g is the first-order rate constant of growth and k_d, of die-off. The solution to Eq. (2.1) is an exponential function, and the population growth exhibits different properties, depending on the relationship between k_g and k_d. If $k_g > k_d$ and x is positive, the biomass increases in an accelerated and unlimited fashion. The latter feature is, of course, nonphysical. When $x = 0$, no dynamics takes place. However, any positive value of the biomass, no matter how small, triggers the runaway growth. We conclude that the equilibrium point $x = 0$ is unstable. Biologically, it means that any number of organisms colonizing the space under consideration can successfully seed a new population. This is frequently the case with simple organisms under favorable growth conditions, *e.g.*, when bacteria are inoculated into warm milk. If, on the contrary, $k_g < k_d$ (and x is still positive), then the biomass shrinks and approaches zero in the limit. This case represents an environment that is unfavorable to the species in question. As before, no dynamics takes place when $x = 0$, but since any positive biomass returns to zero with time, this equilibrium point is now stable with respect to perturbations.

Consider now the case where

$$\frac{dx}{dt} = -k_d x + k_g x^2,$$

(2.2)

$k_d > 0$, and k_g—also positive—is redefined as a second-order rate constant of growth. Whereas the last example was applicable to asexually reproducing organisms (or self-fertilizing hermaphrodites), the case represented by Eq. (2.2) can describe a population reproducing sexually. Since our description remains univariate, it would be appropriate for a population that is well-mixed and has a fixed ratio of sexes or, alternatively, one that consists of obligatorily cross-fertilizing hermaphrodites. Such organisms need to meet to reproduce, and the rate at which organisms meet pairwise can be thought of as being proportional to the second power of the organisms' spatial density (analogously to second-order chemical kinetics reflecting pairwise molecular collisions). Population effects that may arise from spatial variation will be left for a later chapter, and reproduction with defined generations will be considered immediately following this introductory exposition. In the absence of any spatial variation and any consequential age structure, the density of organisms is simply proportional to the population's total biomass, justifying the simple model behind Eq. (2.2).

The properties of the dynamics described by Eq. (2.2) can be deduced by examining the equation's right-hand side. This is a parabolic function of x that has roots at 0 and k_d/k_g. It is negative between these roots and positive elsewhere. Accordingly, the biomass is driven to zero from any value that is smaller than k_d/k_g, and the equilibrium point $x = 0$ is stable. Any starting value that is above k_d/k_g leads to an unrestricted further growth. In other words, a critical seeding mass is necessary to ensure the survival of the population, which is realistic for sexually reproducing organisms. At the same time, the case of Eq. (2.2) still features the unrealistic possibility of population explosion.

The final case in our introductory series of homogeneous models is the one where

$$\frac{dx}{dt} = -k_d x + k_g x^2 - k_i x^3.$$

(2.3)

Here, k_i is introduced as a third-order rate constant of interference between the individuals ($k_i > 0$). The motivation for such an approach is that the population may experience negative effects of crowding, for example, competition for food. The situation captured is the one in which individuals of the population need to meet to interfere with each other. The interference effect of meeting in pairs could be taken into account by adjusting the second-order constant, already named k_g (see Eq. 2.2), which remains a constant of growth as long as the negative effect of meeting in pairs does not outweigh its positive effect on the population. To reflect this situation, we still assume that k_g is positive. The next term capturing the rate of a process whereby individuals meet in space is third-order in x, and the rate constant that reflects its effect on the population biomass is k_i. Higher-order terms may be neglected because

they represent more infrequent events (simultaneous meeting of four or more individuals).

In this case (Eq. 2.3) we again have $x = 0$ as an equilibrium point. Other roots of the right-hand side (the population growth rate function) depend on the values of the rate constants. When $k_g^2 < 4k_dk_i$, there are no other equilibrium points and the rate function is negative for all $x > 0$. In other words, the population cannot be established: $x = 0$ is a stable equilibrium and any starting biomass will eventually die off. If k_g^2 happens to be exactly equal to $4k_dk_i$ (which is improbable but worth considering for completeness), there is a second root, $k_g/(2k_i)$, but the population growth rate is still negative for all $x > 0$ except this one value. The equilibrium point $x = k_g/(2k_i)$ is stable with respect to perturbations that increase x but unstable with respect to perturbations that decrease it and therefore on the whole unstable. We can see that, in essence, the properties established for $k_g^2 < 4k_dk_i$ hold in this special case as well. Finally, if $k_g^2 > 4k_dk_i$, then there are two roots in addition to $x = 0$:

$$x_1 = \frac{k_g - \sqrt{k_g^2 - 4k_dk_i}}{2k_i}, \quad x_2 = \frac{k_g + \sqrt{k_g^2 - 4k_dk_i}}{2k_i}.$$

The growth rate function is negative between 0 and x_1, positive between x_1 and x_2, and negative for $x > x_2$. Zero is therefore still a stable point, as is x_2, but x_1 is unstable. In other words, x_1 represents a critical biomass: any size that is smaller will die off, whereas any that is larger will seed a persistent population which will eventually stabilize at size x_2. This model captures the realistic properties of an isolated, sexually reproducing population of organisms. Its salient properties—whereby stable equilibrium points are separated by unstable equilibrium points, which can all be found without solving the dynamic equations themselves—are common also to more complex and multivariate systems.

Lastly, among the continuous-time univariate models, it is instructive to consider a version in which a zero-order term is present:

$$\frac{dx}{dt} = k_m - k_dx + k_gx^2 - k_ix^3.$$

(2.4)

The constant $k_m > 0$ can represent the rate of migration of organisms into the spatial domain where the biomass is measured—whether active or passively following a flux of the medium in which they reside. The behavior of this model can be visualized qualitatively if we note that it is analogous to the last case, except that to find its equilibria we need to consider not where the three terms dependent on x equal zero but where they equal $-k_m$:

$$-k_dx + k_gx^2 - k_ix^3 = -k_m.$$

(2.5)

Analogously to the roots of the rate function considered in the version without immigration, Eq. (2.5) can be satisfied at one, two, or three values of x. Interesting behavior can be observed when the response of the system to varying the migration

Fig. 2.1 Left-hand side (*solid line*) of Eq. (2.5). In this example, the biomass and time are unitless, $k_g = 1.9$, and $k_d = k_i = 1$. Right-hand side (*dashed line*) is plotted for $k_m = 0.089$ and $k_m = 1.605$
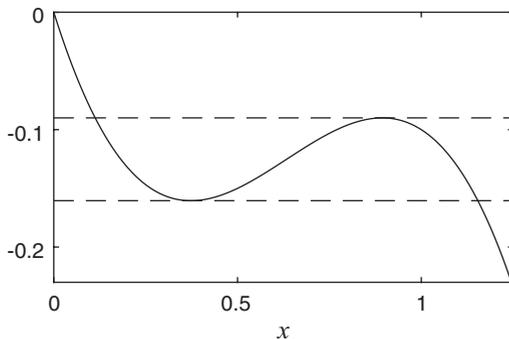
constant is analyzed. The conditions for such behavior arise when the left-hand-side of Eq. (2.5) is negative for all $x > 0$ and has two points where its derivative is zero (Fig. 2.1). The first of these conditions has in fact already been worked out in terms of the rate constants in the last example (amounting to $k_g^2 < 4k_d k_i$), and the second one requires that $k_g^2 > 3k_d k_i$. If k_m is large, immigration can only be balanced by the third-order term (crowding) that dominates at high x; this is the only equilibrium, and it is stable. By decreasing k_m, we can drive the system to a regime where two additional equilibrium points appear to the left of the original one. Of these, the left-most (smallest) is also stable, but the system will remain at the original equilibrium point, because its stability has not changed. Ultimately, however, the original point will meet the unstable point and both will disappear, whereupon the system will spontaneously transition to the remaining equilibrium point at the comparatively small value of x. If we now reverse the direction of change in k_m and drive the system back to the regime with three equilibria in total and two stable ones, it will remain in the left-most equilibrium until this equilibrium disappears by merging with the unstable one. At that point, the system will spontaneously transition to the original, high-biomass steady state. Overall, we observe that the state of the system can depend on the history of the variation in its parameters, and there is a domain in the parameter space where the biomass can follow different trajectories depending on the direction in which the control parameter is varied. Such behavior is termed hysteresis. The classical univariate population study with important hysteresis effects is the budworm outbreak model (Ludwig et al. 1978), to which the reader interested in a more concrete ecological treatment can be referred.

2.2 Growth with Generations: Oscillations and Chaos

Population dynamics characterized by die-off of adult organisms following the breeding season are fairly common across the clades of life and can be presumed to be a shared feature of habitable planets with pronounced seasons. In the simplest

case, biomass x_i of adult organisms of generation i depends only on the biomass observed in the immediately preceding generation:

$$x_i = f\left(x_{i-1}\right).$$

In this instance, equilibria are represented by the roots of $f = 1$. To determine the stability of these equilibria, we can linearize f in the vicinity of each root x^*:

$$\delta_i = x_i - x^*, \qquad \delta_i = \delta_{i-1}\left.\frac{df}{dx}\right|_{x^*}.$$

Since the derivative of f acts on perturbation δ like the factor in a geometric progression through the generations that follow, $|df/dx| < 1$ means that the equilibrium is stable, and $|df/dx| > 1$ means that it is unstable.

Up to this point, the behavior of the models with generations has been analogous to the univariate continuous-time models considered in the last section. However, even the simple model with non-overlapping generations can have qualitatively different regimes in addition to the ones already described. Although the deviation from the equilibrium will eventually die down in all instances of $|df/dx| < 1$, it does so in a monotonic manner only if the derivative is positive. If the derivative is negative, the sign of the deviation from the equilibrium point alternates with each generation. In other words, we would observe damped oscillations around the stable steady state. The manner of the departure from the point of unstable equilibrium can similarly be monotonic or in a form of oscillations of increasing amplitude, depending on the sign of df/dx when $|df/dx| > 1$.

Models with generations can have steady states other than equilibrium points. One of the classical models (May and Oster 1976) has the form

$$x_i = x_{i-1} + k_g x_{i-1} - k_d x_{i-1}^2,$$

where $k_g > 0$ is a growth coefficient and $k_d > 0$ s a die-off coefficient. This model, while it is a finite difference version of the polynomial differential equation models from the last section, reflects a slightly different biology than any of the preceding examples. It is suited to describe reproduction that is not limited by individuals' encounters (positive linear term) but at the same time displays a negative effect of crowding (negative quadratic term). Expressing x in the units of the non-zero equilibrium biomass,

$$\bar{x} = \frac{x}{x^*}, \qquad x^* = \frac{k_g}{k_d},$$

we can see that the dynamics is controlled by a single parameter, k_g:

$$\bar{x}_i = f\left(\bar{x}_{i-1}\right) = \bar{x}_{i-1}\left(1 + k_g\left(1 - \bar{x}_{i-1}\right)\right)$$

We can further note that $df/d\overline{x}$ at $\overline{x} = 1$ (equilibrium) equals $1-k_g$. Thus, the equilibrium is stable for $0 < k_g < 2$ and unstable when $k_g > 2$. To consider the dynamic possibilities afforded by the discrete generations, let us plot f alongside $f^{(2)}$, which is f compounded with itself (*i.e.*, applied sequentially twice). As can be seen in Fig. 2.2—where the bisector indicating the equality of the function value with the argument (*i.e.*, the equality of the reduced biomass $\overline{x}$ one or two generations apart) is also plotted for reference—when k_g approaches 2 from below, $f^{(2)}$ intersects the bisector in the same point as f and its derivative is less than 1. This reflects the fact that biomass size $\overline{x} = 1$ will be stably repeated every two generations as long as it is stably repeated every generation. As k_g crosses above 2, however, the shapes of both f and $f^{(2)}$ indicate a loss of stability at $\overline{x} = 1$. At the same time, two new points arise where $f^{(2)}$ intersects $\overline{x}_i = \overline{x}_{i-2}$. (It is said that a bifurcation takes place.) Each of these points is therefore repeated every second generation. In other words, a two-point cycle is born—a new type of dynamics that is not afforded by univariate models in continuous time. Such a stable cycle, which can attract the trajectory of the system, is referred to as a limit cycle. The slope of $f^{(2)}$ at the two cycle points (Fig. 2.2) is below 1 while being positive, and so demonstrates that each of these points, and therefore the cycle that is comprised of them, is stable.

Continuing to increase k_g in this model, we observe that $df^{(2)}/dx$ at the period-2 stable points decreases until it becomes smaller than -1 (Fig. 2.3). As these points become unstable at period 2, so do they also as points of a degenerate period-4 cycle, as evidenced by the plot of $f^{(4)}$. At the same time, four distinct period-4 stable points are born (Fig. 2.3). Plotting the time course of a simulation starting at some arbitrary biomass size (Fig. 2.4a), we confirm that after a brief initial period, the model trajectory settles into a four-point cycle in which the biomass oscillates about the original "period-1" equilibrium ($\overline{x} = 1$), taking values that alternate above and below it with every new generation. Analysis shows (May and Oster 1976) that
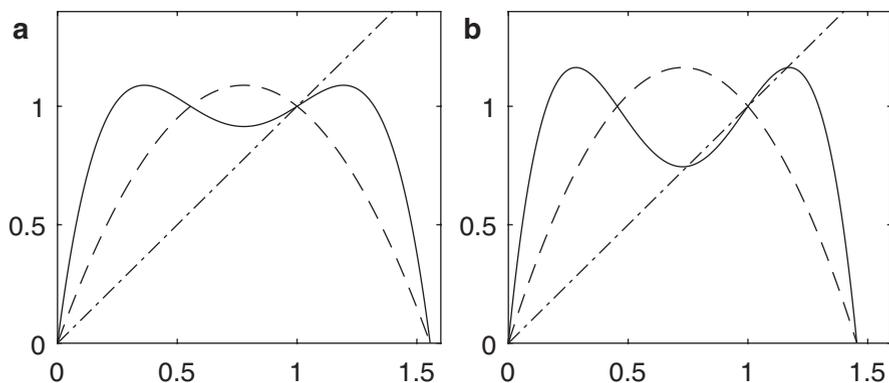

Fig. 2.2 Reproduction function f (*dashed line*) and its second iteration $f^{(2)}$ (*solid line*). The bisector where the function is equal to the argument is plotted for reference (*dash-dot line*). (**a**) $k_g = 1.8$, (**b**) $k_g = 2.2$
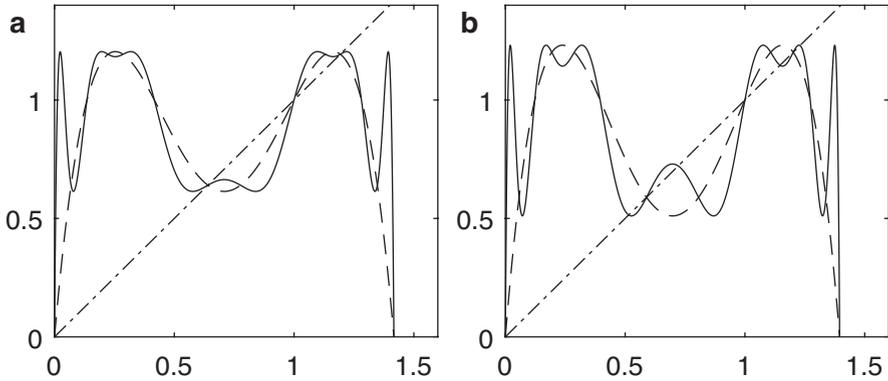
Fig. 2.3 Second-iteration ($f^{(2)}$, *dashed line*) and fourth-iteration ($f^{(4)}$, *solid line*) reproduction function. *Dash-dot line*, bisector for reference. (**a**) $k_g = 2.4$, (**b**) $k_g = 2.53$
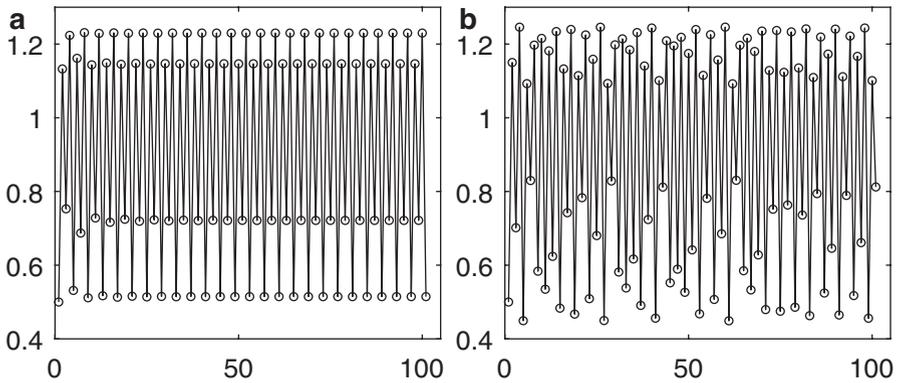

Fig. 2.4 Time course of the model with generations, starting with $\bar{x} = 0.5$. (**a**) $k_g = 2.53$, (**b**) $k_g = 2.6$

period-doubling of this kind continues with the increasing growth parameter, but the parameter intervals leading to each new doubling progressively shorten.

It can be noted that although the standpoint afforded by our knowledge of the dynamics that generate the time series leads us to speak in this case of a single period-4 cycle, a biologist presented by data that have the appearance of the time series in Fig. 2.4a would be equally justified to consider that the dynamics may be that of a comparatively small-amplitude period-4 cycle superimposed on a larger-amplitude period-2 cycle. From such an independent observer's viewpoint, time courses generated with the subsequent period-doubling might appear multiperiodic insofar as the very presence of a repeated pattern remains recognizable.

According to the definition adopted in the mathematical analysis of this type of models, the regime that is called chaotic is reached by the model considered here at around $k_g = 2.57$. Simulating the model with only a somewhat larger parameter