1

History of the *Predator–Prey* Model

Hasty readers who would like to only focus on the mathematical aspects can, if they wish, skip to the next chapter which is logically independent of this one. However, it seems to us that the history of a subject has learning virtues and it would be a shame not to enjoy them. Moreover, the term *history* used in the title is unsuitable. This is not a study of the emergence of concepts and models in the scientific context of their time as a real historical study would require, but more simply the presentation of mathematical models in chronological order of their appearance. These are the models:

– the *logistic* model (1840);

– the *Lotka–Volterra* model (1925);

– the *Gause* model (1936);

– the *Rosenzweig–MacArthur* model (1963);

– the *Arditi–Ginzburg* model (1989).

We will merely make a brief remark on the emergence and reception of the model at the end of each section.

1.1. The logistic model

This section presents a few general ideas and some notations to be used throughout the book.

1.1.1. *Notations, terminology*

A *population* is a set of *identical individuals*.

– *Individuals* can designate inert matter, such as, for example, carbon molecules dissolved in water, or living individuals such as bacteria or complex organisms such as fish or mammals.

– By *identical* we mean that they are identical from a "certain point of view": from the point of view of chemistry, all carbon atoms are identical, but carbon 12 and carbon 14 differ in their atomic nucleus; bacteria belonging to the same species are considered identical as well as bacteria from two different species that have the same growth characteristics.

– The size of a *population* at time t is a real number $x(t)$, which suggests, of course, that the number of individuals is very large so that it can be reasonably represented by a continuous variable. If, for example, our population totals $11,386,749$ individuals and we take one "million individuals" as unit size, then the size will be the real number (with six decimal places) 11.386749. We will come back to this topic.

The size of the population may be the total number of individuals or still the total mass (the mass of each individual multiplied by the number); in the latter case, this is referred to as *biomass*. The number or biomass divided by surface or volume is referred to as *density*. *Resources* encompass everything that is necessary for the growth of individuals in a given population: bacteria consume chemical substances; microalgae consume chemical substances *and light*; viruses "consume" bacteria. The growth rate of individuals, therefore the population growth rate, depends on the presence of various resources. Thereby, we can write:

$$\frac{dx}{dt} = \mu(s_1, s_2, \cdots, s_p)\, x,$$

where the function $(s_1, s_2, \cdots, s_p) \mapsto \mu(s_1, s_2, ..., s_p)$ is the growth rate. The variables $(s_1, s_2, \cdots, s_p)$ represent the quantities of available resources. We may assume that the function μ is increasing in each of its variables, but this is not necessarily the case: there are cases where the increase in resource has

an inhibitory effect. The growth rate can be understood in two ways: taking mortality into account (or disappearance[1]) or not.

REMARK 1.1.– The sentence:

"*the individual growth rate, thus the population growth rate* $(\cdots)$"

deserves all of our attention. What is the "growth rate of an individual"? In the case of a micro-organism it will be the speed with which its biomass increases, divided by its current biomass. Nonetheless, this growth rate, which is a property of individuals, is usually not directly measured. What is more often measured is the population growth, such as, for example, the growth in the diameter of a mold spot: this is the μ of the above expression. It is generally the tendency to identify individual growth rate with that of the population in accordance with the reasoning: if an organization grows by 1% in 1 minute, then the same happens for a population of 10^6 individuals, which will be true only if the 10^6 individuals of the population all have equal access to resources and is not necessarily always the case. For example, for mold, peripheral individuals have more efficient access to the substrate. As shown in this example, there is no reason to assume that the population growth rate is, in general, independent of the size x of the population. As a result, it follows that:

$$\frac{dx}{dt} = \mu(s_1, s_2, \cdots, s_p, x)\, x.$$

This is what will be done when we consider "density-dependent" models.

In many ecologically interesting situations, there is a *limiting resource* which means that all resources except one are in such excess that their possible variation does not affect the value of μ, which is tantamount to assuming that μ only depends on a single variable s (see Remark 3.1 about this topic); if, in addition, we assume a constant mortality rate, we have the model:

$$\frac{dx}{dt} = (\mu(s) - d)\, x.$$

1 The word *disappearance* is ambiguous. Fishes that "disappear" from a population in a lake can also be those that die and those that leave the lake through its outfall.

Assume that s is constant. In this model, either s is such that $\mu(s) > d$ and we have an exponential growth, or on the contrary, $\mu(s) < d$ and we have an exponential decay that leads to extinction. However, the population size acts on the resource as well as on mortality which means that there is no reason for either s or d to be constant. Let us consider some examples.

1.1.2. *Growth with feedback and resource*

1.1.2.1. *Resource is space*

Assume that the population is composed of "plant" individuals. The plants produce seeds that are randomly scattered over a given territory; only the seeds that land on a point of the territory that is not already colonized by a plant can germinate. Let:

– the surface colonizable at time t be: $s(t)$;

– the size of the population be $x(t)$, which can be assimilated to the occupied surface;

– the total available surface be S_T.

Let dt be a small increase in time. We can write:

$$x(t + dt) = x(t) + dt\, \rho\, s(t)\, x(t)$$

to express that the number of seeds that germinate in the time interval dt is proportional to the number of seeds that travel in the atmosphere, thereby to the number of plants "x", proportional to the colonizable surface "s" and to the time period "dt"; ρ is a constant that depends on chosen units. That is, if we evaluate the limit for $dt \to 0$, the differential equation is:

$$\frac{dx(t)}{dt} = \rho\, s(t)\, x(t)$$

and, more simply, if we overlook including time:

$$\frac{dx}{dt} = \rho\, s\, x.$$

Nevertheless, the colonizable surface is:

$$s = S_T - x$$

We thus have a *feedback* of the population on the resource that is of the form:

$$x \mapsto s = \mathcal{R}(x) = S_T - x.$$

In the language of automatic control[2], we are referring to *static feedback* versus *dynamic feedback* where s depends on x through a differential equation (see next section). If, in the growth equation of x, we replace s by its value according to x, we obtain the *loop system* (still in the language of automatic control):

$$\frac{dx}{dt} = \rho\,\mathcal{R}(x)\,x = \rho\,(S_T - x)\,x = \rho S_T x - \rho x^2,$$

which is the well-known "logistic" differential equation that can be rewritten as:

$$\frac{dx}{dt} = r\left(1 - \frac{x}{K}\right)x \qquad [1.1]$$

after establishing $r = \rho\,S_T$ and $K = S_T$.

REMARK 1.2.– The above equation [1.1], as a mathematical object is defined for all x in $\mathbb{R}$ but, in the interpretation that is made thereof as a model of growth of plants on an island, it must be restricted to the interval $[0, K]$ since the area occupied by plants is necessarily positive and smaller than the total area available $K = S_0$.

This remark is not insignificant. Let us reconsider the same model for the same situation and let us introduce an "immigration". What do we mean?

– Imagine that using a process, we are able to colonize a surface $I_m\,dt$ for a time period dt. Taking this assumption into account, the new model would be:

$$\frac{dx}{dt} = r\left(1 - \frac{x}{K}\right)x + I_m,$$

2 Automatic control is the engineering science dedicated to driving (the operation of) complex artificial systems (factories, airplanes, power networks, etc.). Some of its concepts, such as *feedback*, are relevant for the study of complex natural systems such as ecosystems.

which as a differential equation is defined on all $\mathbb{R}^{+*}$. This equation has the globally asymptotically stable equilibrium: $x^* = K\frac{1+\sqrt{1+\frac{4I_m}{rK}}}{2}$ which is strictly greater than K; however, in our interpretation of the model, this value cannot be reached: x must remain less than or equal to K.

– Imagine another situation: during a period dt, an amount $I_m\,dt$ of seeds reach the island; however, only the seeds which will land on the colonizable surface will germinate. In this case, we will write the model:

$$\frac{dx}{dt} = r\left(1-\frac{x}{K}\right)x + I_m(K-x),$$

which still has K as a globally asymptotically stable equilibrium.

In the example we have just chosen, things are very simple and the risk of error is quite low. However, when the situation is a little more complicated, it is easy to make mistakes as discussed in the next section.

1.1.2.2. *The resource is the substrate concentration*

Let us picture micro-organisms (bacteria, yeast, plankton, etc.) that consume a dissolved substrate (a chemical substance). We are assuming that this is a "perfect mixing". "Perfect mixing" means that organisms and substrate concentrations are the same at any point. Let:

– the concentration of substrate at time t be: $s(t)$;

– the micro-organism population concentration at time t be: $x(t)$;

– the initial substrate and micro-organism concentrations be S_0 and x_o.

It is assumed that a constant fraction of substrate molecules that meet an individual of the population is absorbed by the individual; therefore, for a time dt, a quantity proportional to the product of the concentrations is absorbed, that is:

$$s(t+dt) = s(t) - dt\,\rho\,s(t)\,x(t).$$

It is assumed that there is no mortality in micro-organisms and that the mass of the consumed substrate is fully transformed into micro-organism mass[3], we thus have:

$$x(t+dt) = x(t) + dt\,\rho\,s(t)\,x(t).$$

The variable s is not, as in the previous case, *directly* a function of x, but it is the *variation of* s, $s(t+dt) - s(t) = -dt\,\rho\,s(t)\,x(t)$, still corresponding to $\frac{ds}{dt} = -\rho\,s\,x$ which is a function of x. This is then referred to as *dynamic feedback* when we have:

$$\frac{ds}{dt} = \mathcal{R}(s(t), x(t)) = -\rho\,s\,x.$$

In this case, the complete system is simply obtained by combining the two equations, which gives:

$$\begin{cases} \dfrac{ds}{dt} = -\rho\,s\,x \\ \dfrac{dx}{dt} = +\rho\,s\,x \end{cases} \qquad [1.2]$$

However, this system has a clear property (which merely corroborates the hypothesis that all absorbed substrates become biomass) and which, to some extent, brings us back to the previous case. In effect, we have:

$$\frac{d(s+x)}{dt} = 0$$

and thus:

$$s(t) + x(t) = S_o + x_o = M$$

and as a result, we obtain s by static feedback $s = M - x$ and:

$$\frac{dx}{dt} = \rho\,(M - x)\,x \qquad [1.3]$$

3 Normally, we should choose a smaller yield term than 1 given that part of the mass of absorbed substrate is used to maintain the metabolism. Nonetheless, we do not engage in these considerations here because, as it can easily be seen, by carrying out a change of variable a yield equal to 1 can still be attained.

or still;

$$\frac{dx}{dt} = rx(1 - \frac{x}{K}) \qquad [1.4]$$

with: $r = \rho M$ and $M = K$ which is still a logistic equation. It should be noted that this reduction is due to the very simple nature of the model. It would suffice that the mortality of micro-organisms be taken into account so as the model, which becomes:

$$\begin{cases} \dfrac{ds}{dt} = \quad -\rho\, s\, x \\ \dfrac{dx}{dt} = +(\rho\, s\, - m)x \end{cases} \qquad [1.5]$$

cannot be reduced in this way.

REMARK 1.3.– In the reduction which has just been made from systems [1.2] and [1.3], the value M in the reduced system depends on the value of the initial conditions chosen in the entire system and, as in the previous case, equation [1.3] only has meaning as long as x is smaller than M. Assuming that the initial condition is very small, the quantity M can be likened to the initial amount of substrate.

Although it is based on numerous simplifying assumptions: no mortality, no metabolism consumption, a perfect mixing, it turns out that this model is capable of a very good adequacy with reality as evidenced by the adjustment of Figure 1.1, which is taken from a famous article by R. Pearl [PEA 21]. This success of the logistic model has led to excesses, logistics were adapted to anything and, above all, with the pretension that exorbitant properties could be deduced therefrom. Feller reacted against this trend in [FEL 32].

"Carrying capacity"

The two logistic forms: the (r, α)-*model* $\dfrac{dx}{dt} = r\ x - \alpha\ x^2$

or, when defining $K = \frac{r}{\alpha}$: the (r, K)-*model* $\dfrac{dx}{dt} = r\ x \left(1 - \dfrac{x}{K}\right)$

are mathematically completely equivalent.

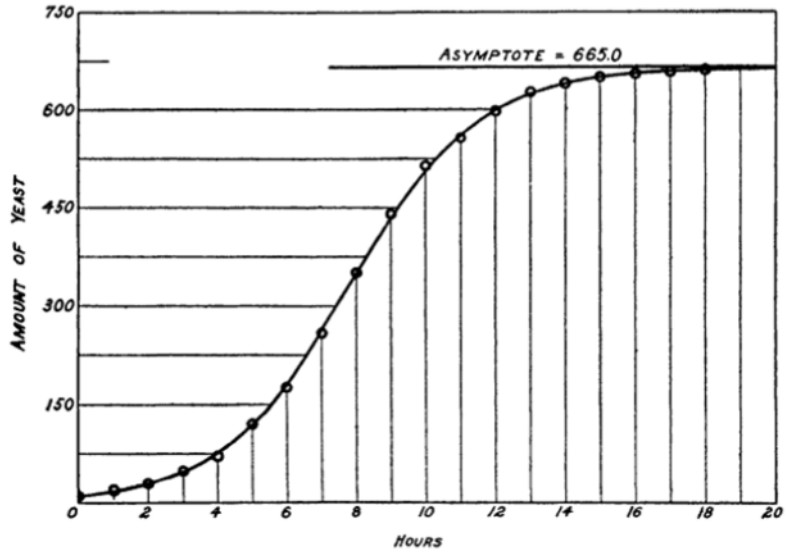

FIG. 1. THE GROWTH OF A POPULATION OF YEAST CELLS

In the publication of this diagram in (8), through an error in proof-reading the abscissal units were stated to be days, when they should have been hours, as is correctly shown here. (Data from Carlson.)

Figure 1.1. *According to Pearl [PEA 21]*

The tradition has long imposed the (r, k)-*model* with the terminology:

– $r =$ *intrinsic growth rate*;

– $K =$ *carrying capacity*.

This terminology is understood in the context of the previous interpretations where the total area of the island or the initial amount of substrate can actually be considered as a carrying (in terms of biomass) capacity (maximum possible) of the medium. Nonetheless, this terminology raises a few problems that we will review in section 1.1.4.

1.1.3. *Another interpretation of the logistic equation: the interference between individuals*

In the two derivations that we have just made of the logistic equation, we have explicitly introduced the hypothesis that the growth rate (incorporating

"reproduction" and "disappearance"[4]) of our population depended on a variable resource which, in turn, directly or indirectly depended on the population density.

Now, consider a population whose growth rate r is constant. In the absence of any other phenomenon, growth is exponential. To limit this growth, we introduce a "disappearance" term proportional to x^2:

$$x(t+dt) = x(t) + dt[rx - \alpha x^2] \qquad [1.6]$$

that we justify as follows.

We assume that individuals that constitute the population reside within a given limited space and move in a perfectly random manner as Brownian particles do (this is the hypothesis of perfect mixing). The size of the population is represented by density $x(t)$. Individuals are going to encounter one another. For a time period dt, the number of encounters will be proportional to the product of concentrations: $a\ \ x(t) \times x(t) \times dt$ (for a particular individual, the number of encounters is proportional to the size of the population, and therefore the total number of encounters is proportional to the square $x^2(t)$). Now, imagine that the encounter of two individuals results, with a certain probability, in the destruction of one or both individuals. For a period dt will thus disappear:

$$\rho\ a\ x^2(t)dt$$

individuals which will have to be subtracted from the $rx(t)dt$ individuals of the exponential growth, where ρ is a parameter that measures the lethality of the encounter. We thus obtain the relationship [1.6], which we can rewrite by passing to the limit on $dt \to 0$ and defining $\alpha = \rho\, a$:

$$\frac{dx}{dt} = r\ x(t) - \alpha\ x^2(t) \qquad [1.7]$$

or still, if we define that $K = \frac{r}{\alpha}$:

$$\frac{dx}{dt} = r\ x\left(1 - \tfrac{x}{K}\right) \qquad [1.8]$$

4 Which includes mortality and/or leaving the domain as in a bioreactor.

We see that in this interpretation, the notion of "carrying capacity" (of the medium) is inadequate. Changing α, which is a parameter rather describing a property of the *population* (the probability of encounters and their lethality), would change the "carrying capacity" which is a property of the *medium*.

1.1.4. *(r, α)-model or (r, K)-model?*

Levin's paradox [HUT 78]. Consider a situation where for a given positive carrying capacity K, the individual growth rate r is negative. Therefore, for an initial condition greater than K the solutions of [1.7] tend to infinity; whereas for a smaller initial condition than K, they tend to 0. This is obviously an absurd situation that makes some people say that the logistic equation can only be applied for $r > 0$.

In fact, what is absurd is the simultaneous consideration of a negative growth rate, therefore a population that can only disappear and a positive "carrying capacity": carrying capacity of what? It can be seen that "carrying capacity" cannot be a property of the medium alone, independent of the population received. In the (r, α)-*model*, if r is negative and if the result of the interaction $\alpha = \rho\ a$ is positive (lethality is positive), the population decreases to 0; in other words, negative growth rate and positive lethality require a negative K and the disappearance of the paradox.

The Ginzburg paradox [GIN 92]. Imagine fish in a lake described by the (r, K)-model and a fishing business carrying out constant extraction:

$$\frac{dx}{dt} = r\ x \left(1 - \frac{x}{K}\right) - \mu.$$

The intuition is that if K is the "carrying capacity", there is no reason for not reaching the latter, it will simply be more slowly achieved due to the extraction. In fact, this is not what the above equation states as it gives two solution equilibria to the second degree equation:

$$-\frac{rx^2}{K} + r\ x - \mu = 0$$

the smallest being unstable and the biggest being stable. The extraction, which does not alter the medium, thus modifies its "carrying capacity". The (r, α)-*model* that has no concept of "carrying capacity" eliminates the paradox.

The paradox of two sites. We consider the following model for two sites between which a population can migrate.

$$\begin{aligned} \frac{dx_1}{dt} &= r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) + \beta(x_2 - x_1) \\ \frac{dx_2}{dt} &= r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) + \beta(x_1 - x_2) \end{aligned} \qquad [1.9]$$

If there is no migration at each site, the equilibrium is K_1 and K_2 and it can be considered that, in the absence of migration, the "total carrying capacity" of both sites together is $K_1 + K_2$. We now assume that we are faced with the specific situation in which:

$$r_1 = \rho K_1 \qquad \text{and} \qquad r_2 = \rho K_2$$

The parameter β is the migration rate from one site to the other, identical in both directions. The system [1.9] has equilibria:

$$(0,0); \quad (K_1,0); \quad (0;K_2); \quad (x_1^*(\beta), x_2^*(\beta))$$

with $x_1^*(\beta) > 0, x_2^*(\beta) > 0$ and $x_1 \neq x_2$. The existence of this last equilibrium can be easily seen by drawing the graphs of the two parabolas of equations:

$$\begin{aligned} \rho K_1 x_1 \left(1 - \tfrac{x_1}{K_1}\right) + \beta(x_2 - x_1) = 0 \\ \rho K_2 x_2 \left(1 - \tfrac{x_2}{K_2}\right) + \beta(x_1 - x_2) = 0 \end{aligned} \qquad [1.10]$$

Given the equilibrium $(x_1^*(\beta), x_2^*(\beta))$, it satisfies [1.10] which leads to:

$$\begin{aligned} \rho x_1^* \left(K_1 - x_1^*\right) = \beta(x_1^* - x_2^*) \\ \rho x_2^* \left(K_2 - x_2^*\right) = \beta(x_2^* - x_1^*) \end{aligned} \qquad [1.11]$$

then dividing by ρx_i^*:

$$\begin{aligned} K_1 - x_1^* = \frac{\beta(x_1^* - x_2^*)}{\rho x_1^*} \\ K_2 - x_2^* = \frac{\beta(x_2^* - x_1^*)}{\rho x_2^*} \end{aligned} \qquad [1.12]$$

Adding the two equations, it follows that:

$$x_1^* + x_2^* = K_1 + K_2 + \frac{\beta(x_2^* - x_1^*)}{\rho x_1^*} + \frac{\beta(x_1^* - x_2^*)}{\rho x_2^*} \qquad [1.13]$$

which finally yield, after reduction to the same denominator:

$$x_1^* + x_2^* = K_1 + K_2 + \frac{\beta(x_2^* - x_1^*)^2}{\rho x_1^* x_2^*} \qquad [1.14]$$

The total biomass at equilibrium $x_1^* + x_2^*$ is thus strictly greater than the sum of "carrying capacities". Once again, the "total carrying capacity" (of both sites) depends on a property of the population: its capability to migrate. There is a more serious problem though. Assume that the interpretation of our two coupled logistic models be that of section 1.1.2.2. In case of no migration, the equilibrium at each site is $S_{o,1} + x_{o,1}$ and $S_{o,2} + x_{o,2}$ and it is absurd that the total biomass at equilibrium be greater than the sum of these two biomasses. Whether there is migration or not, there is conservation of mass. The error originates from the fact that, if we adopt this interpretation of the logistic, we must imperatively add constraints $x_i \leq K_i = S_{o,i} + x_{o,i}$ to the model. The equilibrium $(x_1^*(\beta), x_2^*(\beta))$ does not respect these constraints.

On the contrary, if our interpretation of the logistic equation is that of section 1.1.3, there is no longer any problem: migration may well have the effect of increasing the total biomass at equilibrium. Consider, for example, two islands of surface S_1 (large) and S_2 (small) and assume that on S_1, the growth rate r_1 is very small (or even zero) and large on S_2. The interference rate α_1 is small on S_1 (individuals are not likely to encounter each other) and large on S_2 (there is little space, individuals often encounter). In both cases, the biomasses at equilibrium in the absence of migration are small but for different reasons: small growth rate on S_1 and lack of space on S_2. Migration is a means to "enjoy" the benefits of each site.

To conclude this section, we will assert that when using the logistic equation:

– it is necessary to explain the variation range of the variable x and, according to the case, write:

$$\frac{dx}{dt} = r\, x(t) - \alpha\, x^2(t) \qquad 0 \leq x < +\infty \qquad [1.15]$$

– or still:

$$\frac{dx}{dt} = r\ x(t) - \alpha\ x^2(t) \qquad 0 \leq x \leq \frac{r}{\alpha} \qquad [1.16]$$

– and overlook the expression "carrying capacity" which is better replaced with "biomass at equilibrium" which is rather neutral.

In the following, except where the contrary is explicitly mentioned, logistic designates the model [1.15] in which the variable x is not upper bounded.

1.1.5. *Historical notes and criticisms*

The invention of the logistic equation in 1838 is attributed to P. F. Verhulst. In mathematical terms, it was no matter for concern, even at that time, but since it was already raising the issue regarding the meaning of mathematical modeling, huge amounts of literature have been dedicated to it. Recently, discussions have been reinitiated because of the debate known as the "SLOSS debate". SLOSS is an acronym for Single Large Or Several Smalls: when a natural reserve is established to preserve biodiversity, is it preferable to implement a single large reserve or to split it into several pieces between which species can migrate? (see [HAN 99]). One will find recent contributions to this issue in [ARD 15, ARD 16, ARD 18].

1.2. The Lotka–Volterra *predator–prey model*

1.2.1. *The model*

In its interpretation of section 1.1.2, the logistic equation represented the growth of a consumer of a resource *fixed once and for all*. The next step is to figure out *dynamic* resource. The resource is now a population which is exponentially growing (we may consider bacteria in an "inexhaustible" medium which is not explicit and which are in turn consumed by other micro-organisms). The Lotka–Volterra *predator–prey* model refers to the system:

$$\begin{cases} \dfrac{dx}{dt} = rx - axy \\ \dfrac{dy}{dt} = bxy - my \end{cases} \qquad [1.17]$$

where all the coefficients are strictly positive, the variable x is the amount of *prey* or *resource*, variable y of *predators* or *consumers*. In the absence of *consumer*, the *resource* exponentially increases with a constant growth rate r. If x and y are concentrations of individuals, the term axy is proportional to the *encounter probability* of a *resource* individual with a *consumer* individual (a "prey" and "predator"); the minus sign in the equation is interpreted by saying that the encounter is followed by partial or total disappearance of the *resource* individual. The *consumer* population, when there are no resources, decreases exponentially with a mortality rate m. The positive term bxy in the second equation can be interpreted by stating that what has been taken from the *resource* population following the encounter of two individuals is recovered as individual or "portion of individual" of the *consumer* population. The difference between the two coefficients a and b is interpreted, on the one hand, in terms of "yield" (1 kg of consumed prey does not become 1 kg of predator) and, on the other hand, by the fact that the units to measure each quantity may differ. Moreover, by changing the value of the units, it is possible to recover the model:

$$\begin{cases} \dfrac{dx}{dt} = r\,(1-y)\,x \\ \dfrac{dy}{dt} = m\,(x-1)\,y \end{cases} \qquad [1.18]$$

which we will analyze now.

1.2.2. *Model analysis*

The two-equation system [1.18] possesses the two equilibria: $(0,0)$ and $(1,1)$. The first corresponds to the absence of both populations. The Jacobian matrix (see Appendix for a reminder on the stability of equilibria and the Jacobian matrix) at equilibrium $(0,0)$ is:

$$\begin{pmatrix} r & 0 \\ 0 & -m \end{pmatrix} \qquad [1.19]$$

The origin is a saddle point whose stable and unstable trajectories are respectively $t \mapsto (0, \mathrm{e}^{-mt})$ and $t \mapsto (\mathrm{e}^{rt}, 0)$. The Jacobian matrix at equilibrium $(1, 1)$ is:

$$\begin{pmatrix} 0 & -r \\ m & 0 \end{pmatrix} \qquad [1.20]$$

The two eigenvalues are $\pm i\sqrt{rm}$ and as such the linear approximation at this point is a center. In fact, we will see that all the trajectories of strictly positive initial conditions are closed curves that surround the equilibrium $(1, 1)$ and, therefore, that the equilibrium $(1, 1)$ is a center for the system [1.18] itself. For this purpose, we will show that this system has a first integral $V(x, y)$[5], and that the level curves of this function are closed curves that surround the point $(1, 1)$ and finally that these curves are entirely travelled in the direct direction.

The first integral. The function:

$$(x, y) \mapsto V(x) = m(x - \ln(x)) + r(y - \ln(y))$$

is constant along the trajectories of [1.18]. In effect, we compute:

$$\frac{\partial V}{\partial x}\frac{dx}{dt} + \frac{\partial V}{\partial y}\frac{dy}{dt} \qquad [1.21]$$

that is:

$$\left(m - \frac{m}{x}\right)(rx - rxy) + \left(r - \frac{r}{y}\right)(-my + mxy) = 0. \qquad [1.22]$$

Therefore, if:

$$t \mapsto (x(t), y(t))$$

is a solution of [1.18], we correctly have:

$$V(x(t), y(t)) \equiv C$$

5 That is, a constant function along the trajectories of the system.

or, in other words, the paths of [1.18] are drawn on the level curves of the function $V(x, y)$.

First integral level curves. We will describe Volterra's graphic procedure which allows us to visualize the level curves of the function V. The relation:

$$V(x(t), y(t)) \equiv C$$

is written as:

$$m(x - \ln(x)) + r(y - \ln(y)) = C$$

or:

$$x - \ln(x) = \frac{r}{m}(-y + \ln(y)) + \frac{1}{m}C$$

or, more simply:

$$x - \ln(x) = \frac{r}{m}(-y + \ln(y) + C')$$

with $C = rC'$.

In Figure 1.2, respectively in red and blue, we have plotted the graphs of the functions:

$$x \mapsto z = x - \ln(x)$$
$$y \mapsto z = \frac{r}{m}(-y + \ln(y) + C')$$

for some value of the constant C'. Let us choose x; it defines z such as $z = x - \ln(x)$. Let us look for the y such that $\frac{r}{m}(-y + \ln(y) + C') = z$. They are defined by the intersection of the blue graph with the red horizontal of z-ordinate z. For values of x neither too small nor too big, there are two such values denoted y_1 and y_2 in the figure. These two values are projected, according to the vertical axis, to obtain the two points of coordinates (x, y_1) and (x, y_2) for which $V(x, y_1) = V(x, y_2) = mC'$.

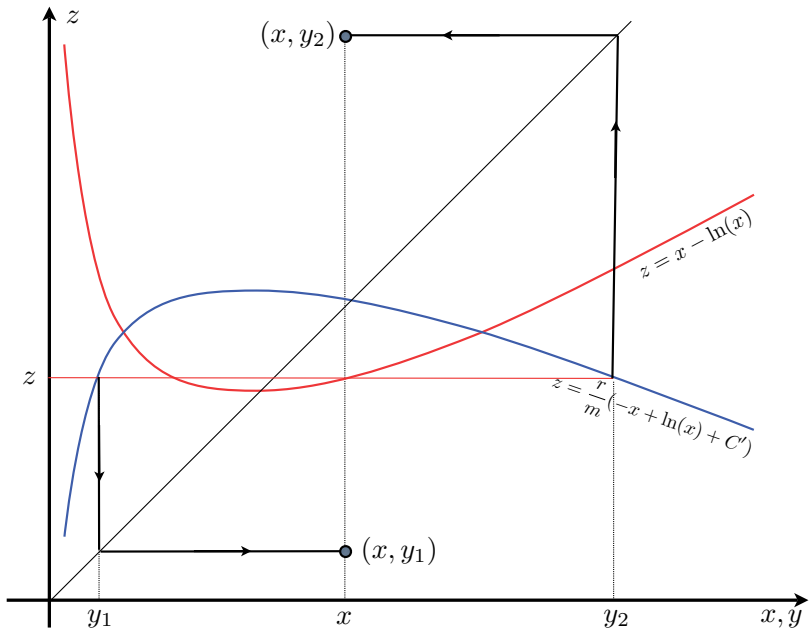

Figure 1.2. *The Volterra process. For a color version of this figure, see www.iste.co.uk/lobry/consumer.zip*

In Figure 1.3, we have repeated the previous construction for a determined number of values of x which gave the (round) points, then joined by a closed curve. It can easily be observed that the curve of level $V(x, y)$ is a closed curve. Furthermore, let us vary x of the value a which corresponds to the minimum of the red graph, to the value b which is the largest possible value for which y can be found such that $V(x, y) = C$. The corresponding value of $z = x - ln(x)$ will grow and the point $x, z = x - \ln(x)$ travels the red arc from A to B. The point (y_2, z) will traverse the blue arc from α towards β and, finally, the couple (x, y_2) traverses the black arc from $\mathcal{A}$ to $\mathcal{B}$. We can guess how to build three other arcs that will form the black closed curve. By varying the constant C, we obtain a family of concentric closed curves that surround the point of coordinates $(1, 1)$ and fill the whole positive orthant.

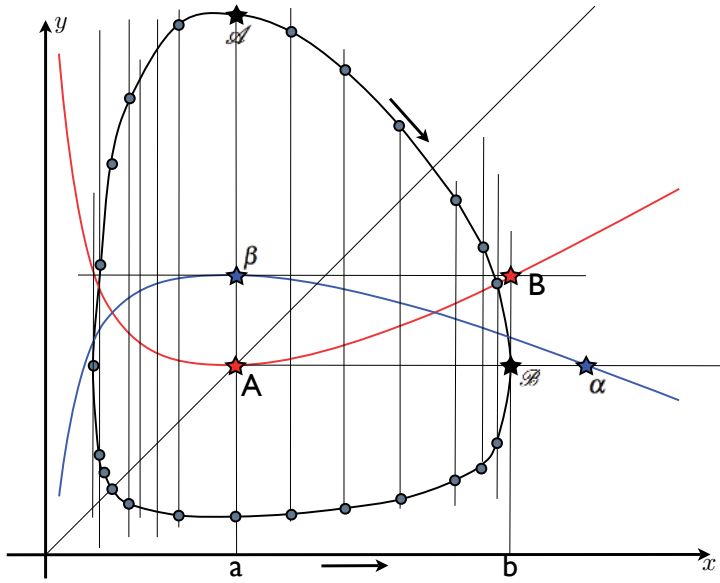

Figure 1.3. *Plot of isovalues. For a color version of this figure, see www.iste.co.uk/lobry/consumer.zip*

1.2.3. *Phase portrait and simulations*

Since the only non-zero equilibrium of the system [1.18] is the point of coordinates (1.1), a solution of initial condition located on one of the level curves will traverse it completely and return to its starting point. All solutions are therefore periodic solutions. In Figure 1.4, a few simulations are represented for the particular case of the system:

$$\begin{cases} \dfrac{dx}{dt} = 3\,(1-y)\,x \\ \dfrac{dy}{dt} = (-1+x)\,y \end{cases} \qquad [1.23]$$

and, in Figure 1.5, a simulation of a trajectory in a "time" system of coordinates (namely x and y according to time). The systematic phase shift between the extremums of x and y should be brought to attention. This is not specific to the system being studied but a general property of any periodic solution of a differential system in dimension two.

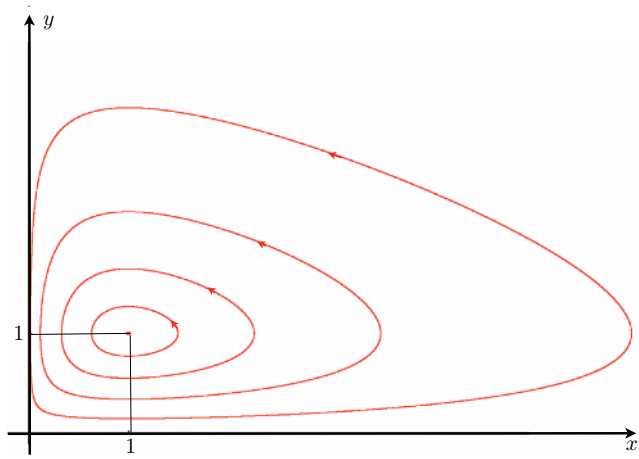

Figure 1.4. *Simulations of system [1.23]. For a color version of this figure, see www.iste.co.uk/lobry/consumer.zip*

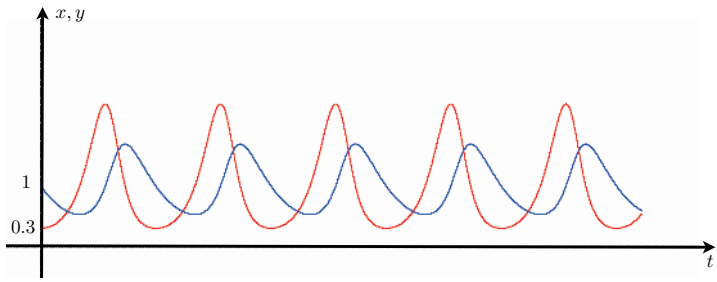

Figure 1.5. *Simulations of system [1.23]. For a color version of this figure, see www.iste.co.uk/lobry/consumer.zip*

1.2.4. *Historical notes and criticisms*

In Figure 1.6, we can read how A.J. Lotka (1880–1949) in 1920 in [LOT 20] justified the equations of the model that bear his name associated with Volterra's. Lotka was a chemist and had been interested in oscillating chemical reactions. At the same time[6], the mathematician V. Volterra

6 There is ongoing disagreement about priority on these issues. On this matter, [ISR 96] should be referred to.

(1860–1940) showed interest in biology, particularly[7] to the dynamics of populations. In Figure 1.7, Volterra explains how he justifies his model, and in Figure 1.8, he exposes its graphical method which proves that trajectories are periodic. While Lotka (inspired by chemistry) was satisfied that his model produced oscillations, Volterra did not seem particularly interested by this aspect but rather by the fact that the average biomass value over a cycle is constant and by the reaction of the value of these biomasses to an external disturbance (such as fishing) [VOL 27, VOL 28, VOL 36, DAN 35].

We now proceed to consider a simple special case, as follows:
The system comprises

1. A species of organism S_1, a plant species, say, deriving its nourishment from a source presented in such large excess that the mass of the source may be considered constant during the period of time with which we are concerned.

2. A species S_2, for example a herbivorous animal species, feeding on S_1.

In this case we have the following obvious relations

$$\left.\begin{array}{l}\text{Rate of increase of } X_1 \\ \text{per unit of time}\end{array}\right\} = \left\{\begin{array}{l}\text{Mass of newly} \\ \text{formed } S_1 \text{ per} \\ \text{unit of time}\end{array}\right\} - \left\{\begin{array}{l}\text{Mass of } S_1 \\ \text{destroyed by} \\ S_2 \text{ per unit of} \\ \text{time}\end{array}\right\} - \left\{\begin{array}{l}\text{Other dead} \\ \text{or excretory} \\ \text{matter elimi-} \\ \text{nated from } S_1 \\ \text{per unit of} \\ \text{time}\end{array}\right\} \quad (3)$$

$$\left.\begin{array}{l}\text{Rate of increase of } X_2 \\ \text{per unit of time}\end{array}\right\} = \left\{\begin{array}{l}\text{Mass of newly} \\ \text{formed } S_2 \text{ per} \\ \text{unit of time} \\ \text{(derived from} \\ S_1 \text{ as food in-} \\ \text{gested)}\end{array}\right\} - \left\{\begin{array}{l}\text{Mass of } S_2 \\ \text{destroyed or} \\ \text{eliminated per} \\ \text{unit of time}\end{array}\right\}$$

Or, in analytical symbols,

$$\begin{aligned}\frac{dX_1}{dt} &= A'_1X_1 - B_1X_1X_2 - A''_1X_1 \\ &= (A'_1 - A''_1)X_1 - B_1X_1X_2 \\ &= A_1X_1 - B_1X_1X_2 \\ &= X_1(A_1 - B_1X_2) \\ \frac{dX_2}{dt} &= A_2X_1X_2 - B_2X_2 \\ &= X_2(A_2X_1 - B_2)\end{aligned}$$

Figure 1.6. *Excerpt from Lotka's article in 1920*

7 Influenced by his son-in-law, the marine biologist U. D'Ancona (1896–1964).

§ 3. Association of two Species one of which feeds upon the other.

1. Let N_1 and N_2 be the numbers of individuals of the two species. Let $\varepsilon_1 > 0$ represent the coefficient of increase which the first would have if the other did not exist. Let us suppose that the second would die out because of lack of food if it were alone; therefore let its coefficient of increase be negative and equal to $-\varepsilon_2$ (ε_2 can be considered as a coefficient of decrease). If each of the two species were alone we should have

$$[7_1] \quad \frac{dN_1}{dt} = \varepsilon_1 N_1, \qquad [7_2] \quad \frac{dN_2}{dt} = -\varepsilon_2 N_2.$$

But if they are together and the second species feeds upon the first ε_1 will diminish and $-\varepsilon_2$ will increase, and evidently the more numerous the individuals of the second species become the more ε_1 will diminish, and the more the individuals of the first species increase, the more will $-\varepsilon_2$ increase. To represent this fact in the simplest manner let us suppose that ε_1 diminishes proportionally to N_2, that is by the amount $\gamma_1 N_2$, and that $-\varepsilon_2$ increases proportionally to N_1, that is by the amount $\gamma_2 N_1$.

We shall have then the differential equations

$$(A_1) \quad \frac{dN_1}{dt} = (\varepsilon_1 - \gamma_1 N_2) N_1, \qquad (A_2) \quad \frac{dN_2}{dt} = (-\varepsilon_2 + \gamma_2 N_1) N_2.$$

Figure 1.7. *Excerpt from Volterra's article in 1928*

An initial criticism that can be made of this model is that, in the absence of consumer, the resource exponentially increases. It would probably be preferable that growth have a dynamic of the logistic type. It can also be noted that this model is not "*robust*"[8]: a very small disturbance in the equations could destroy the family of periodic trajectories surrounding the equilibrium. Finally, the amplitude of the oscillations depends on the initial condition: a permanent behavior would be preferable which, as in the case of the logistic equilibrium, would be intrinsic.

8 In mathematical terms, the definition of *structurally stable* (see Chapter 5) clearly reflects this idea.

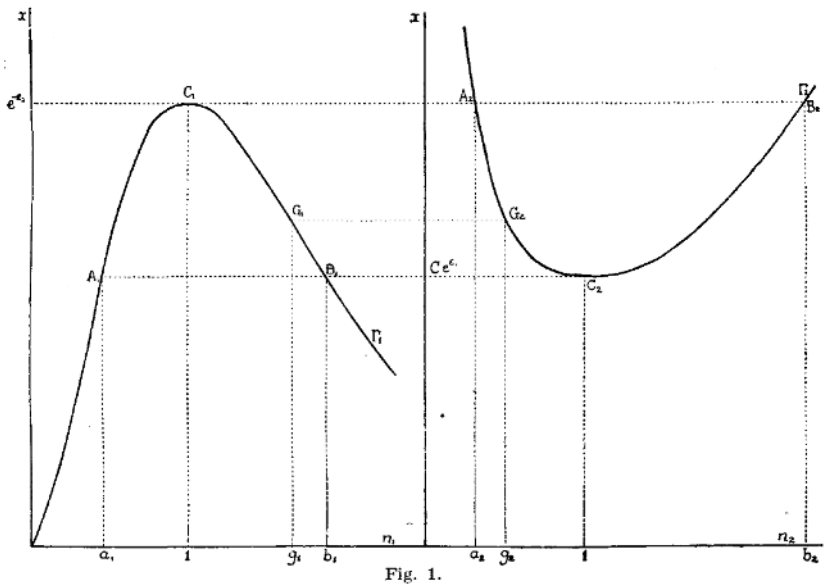

Fig. 1.

arranged the two curves as in fig. 1, with one axis of abscissas the continuation of the other, let us draw the normals to x from the vertices C_1 and C_2 and consider the sections $A_1C_1B_1$, $A_2C_2B_2$ of the two curves lying between these two parallels. Let $a_1 < 1$ and $b_1 > 1$ be the abscissas of A_1 and B_1, $a_2 < 1$, $b_2 > 1$ the abscissas of A_2 and B_2.

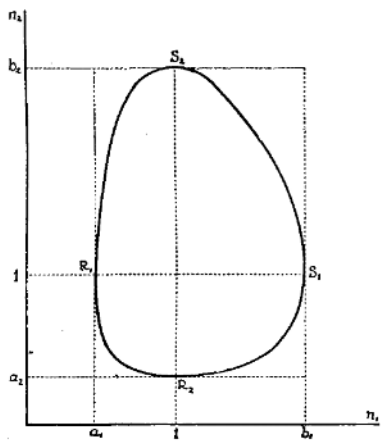

Fig. 2.

Then let us try to construct the curve λ having n_1 for abscissa and n_2 for ordinate. First let us make the point A_2 correspond to the point C_1 and trace the arc C_1B_1 with the point G_1. Then in the curve Γ_2 let us trace the arc A_2C_2, and, corresponding to G_1 on Γ_1 we shall have G_2 on Γ_2, on the same perpendicular to x. Then the value $n_2 = g_2$ will correspond to $n_1 = g_1$, g_1 and g_2 being respectively the abscissas of G_1 and G_2. Then while n_1 increases from 1 to b_1, n_2 will increase from a_2

Figure 1.8. *Volterra's graphic method*

Remarkably, A.N. Kolmogorov had partly responded to these criticisms in a short article [KOL 36] as early as 1936. However, the mathematical ideas of Kolmogorov were very ahead of his time, because they put forward questions of qualitative dynamics and structural stability: basically, he showed that the typical situation for a predator–prey model is to have a stable equilibrium or a limit cycle.

Nevertheless, we will mainly point out the following criticism, which is more recent since it assumes that a computer is being used and which highlights the limits of the representation of the dynamics of a population using differential equations. Let us reconsider the examination of Figure 1.4. We can observe that the outermost trajectory follows very closely "along" the vertical axis. If we consider trajectories that surround this latter, we will necessarily get closer to the axis and the variable $x(t)$ will assume smaller and smaller values. What would happen in a more quantitative way? If we assume as initial condition $(x_o, y_o) = (0.01, 0.01)$ and if we integrate on more than one full turn, the computer will output as a minimum value of $x(t)$, the value:

$$\min_{x(t)} = 0.000000019 = 1.9\,10^{-8}$$

which raises a real modeling problem. Furthermore, assume that our system represents a reality where a unit of x is equivalent to 10^6 individuals. Our initial condition of $(0.01, 0.01)$ corresponds to $10,000$ individuals of the prey population and the minimum reached will be less than *two hundredths* of an individual before growing again! Provided with reasonable initial conditions, the Lotka–Volterra model associates trajectories with which the model eventually stops making any sense. This is what is known as the *atto-fox problem* covered in more detail in Chapter 4.

1.3. The Gause model

1.3.1. *The model*

In the Lotka–Volterra model of section 1.2.1, the resource extraction term:

$$-bxy$$

is linear in the resource x. This means that when the amount of resource doubles, the same happens with the extraction, if it is multiplied by ten so is

the extraction, which is not realistic. There is inevitably a limit to the consumer capability to extract. Gause proposed to replace this linear term by:

$$\begin{aligned} \text{if } x > \alpha \text{ then} : \mu(x) &= \frac{\mu_{\max}\, x}{e + x} \\ \text{otherwise} : \mu(x) &= 0 \end{aligned} \qquad [1.24]$$

where the constants α, μ and e are strictly positive. For $x > \alpha$, the form of $\mu(x)$ expresses saturation. In effect, when x tends to infinity $\mu(x) = \frac{\mu_{\max} x}{e+x}$ increases towards the finite limit: $\mu_{\max}$. On the contrary, the condition $x \leq \alpha \Longrightarrow \mu(x)y = 0$ expresses that if the resource is too rare, there is no possible extraction. This is what is called a *refuge effect*[9]. Therefore, structurally, with regard to its variable x, this model is immune to the atto-fox problem.

Besides this new form of the resource extraction term, the assumptions of resource exponential growth and consumer exponential decay are preserved. This gives us the model:

$$\begin{aligned} \frac{dx}{dt} &= rx - \frac{1}{Y}\mu(x)y \\ \frac{dy}{dt} &= (\mu(x) - m)y \\ x > \alpha &: \mu(x) = \frac{\mu_{\max}\, x}{e + x} \\ x \leq \alpha &: \mu(x) = 0 \end{aligned} \qquad [1.25]$$

where Y is a term that expresses the yield and that we chose to be equal to 1 later in this section[10].

At first glance, this model is a mathematical problem: the right member of the equation is discontinuous! Moreover, theorems about differential equations generally state that second members must be continuous and even more. What does "the derivative of $x(t)$ is equal to something that depends discontinuously on $x(t)$" mean? Such a presentation does not easily answer the question, but

9 If the resource is a species of bacteria producing a biofilm, it could occur that, for low concentrations, bacteria remain included in the biofilm which would make them inaccessible to the consumer.

10 This can always be achieved by means of properly choosing the units' value.

it should be remembered that the differential equation $\frac{dx}{dt} = f(x) \quad x(0) = x_o$ represents the limit $dt \to 0$ of the sequence:

$$x(t + dt) = x(t) + dt\, f(x(t)) \qquad x(0) = x_o \qquad [1.26]$$

where the fact that f presents a discontinuity is not a problem. In case it is desirable to program the discontinuity of μ, we will simply write the conditional loop:

$$\textit{If } x > \alpha \textit{ then } \mu := \tfrac{\mu_{\max} x}{e+x} \textit{ else } \mu := 0\ ;$$

This point is developed in the appendix.

1.3.2. *Model simulations*

We will see the accurate mathematical study of this model in the next chapter and here we just comment on two simulations from which we will see that they are representative.

COMMENTS ABOUT FIGURE 1.9.– The simulated model is:

$$\begin{aligned} &\tfrac{dx}{dt} = 0.6\, x - \mu(x) y \\ &\tfrac{dy}{dt} = (\mu(x) - 0.5) y \\ &x > 0.1 : \mu(x) = \frac{x}{1 + 0.1\, x} \\ &x \leq 0.1 : \mu(x) = 0 \end{aligned} \qquad [1.27]$$

When $x > 0.1$, we have $\mu(x) = \frac{x}{1+0.1x}$ which thus appears as a small disturbance of $\mu(x) = x$ as long as x is not too large; unsurprisingly, the trajectories are close to the periodic trajectories of the Lotka–Volterra system corresponding to $\mu(x) = x$. However, these are no longer periodic trajectories but spirals that depart from the equilibrium $x^* = 0.525$ and $y^* = 0.632$. The straight line $x = 0.1$ is plotted in green, which corresponds to the threshold. The trajectory originating from point a, due to constantly getting away from the origin, eventually meets the line $x = 0.1$ at point a'. Then, the trajectory goes down along the line $x = 0.1$ and leaves to the right immediately after crossing the isocline of the x.

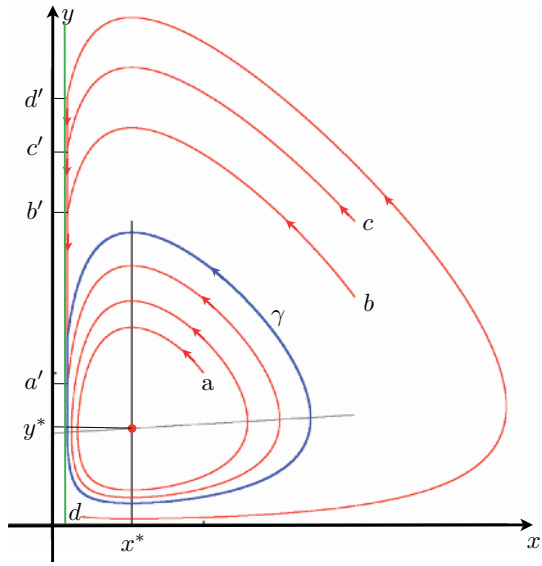

Figure 1.9. *Model [1.28]: existence of a limit cycle. For a color version of this figure, see www.iste.co.uk/lobry/consumer.zip*

This behavior along $x = 0.1$ can be understood in the following way. If we consider the region above the isocline of the x and just a little bit (of the order of a small amount compared to dt, where dt is the integration step) to the right of $x = 0.1$, we have $\frac{dx}{dt} < 0$ and, at the following step, we shift to the left of $x = 0.1$. However, then we have $\frac{dx}{dt} = 0.6\,x > 0$ and, in the next step, we will shift back to the right of $x = 0.1$, and so on. We are thereby oscillating between the right and the left of $x = 0.1$. Since we are to the left of the isocline of the y, the vertical speed is negative and therefore $y(t)$ is decreasing as long as we are above the isocline of the x. Beyond the isocline of the x, whether considering the right- or the left-hand side of $x = 0.1$, we have $\frac{dx}{dt} > 0$, so at each step we are moving away on the line of $x = 0.1$.

All trajectories originating from b, c and d, eventually meet the line $x = 0.1$ at the points of ordinate b', c' and d', they follow downwards along the line $x = 0.1$ and leave it at the same point as before as soon as they meet the isocline of the x. The trajectory originating from this point is traced in blue which, after achieving a circle around the equilibrium, will eventually follow again along $x = 0.1$. All trajectories meet the periodic solution that we have just defined in finite time. There is a *limit cycle*.

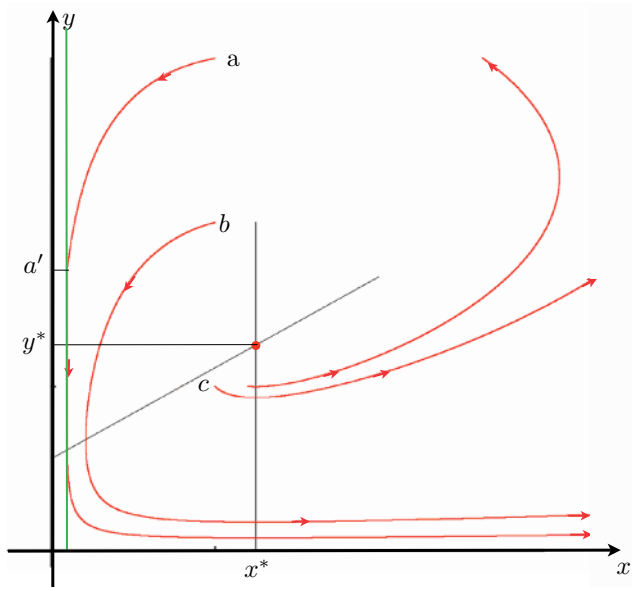

Figure 1.10. *Model [1.25]: unbound trajectories. For a color version of this figure, see www.iste.co.uk/lobry/consumer.zip*

COMMENTS ABOUT FIGURE 1.10.– The simulated model is:

$$\begin{aligned}
&\frac{dx}{dt} = x - \mu(x)y \\
&\frac{dy}{dt} = (\mu(x) - 1)y \\
&x > 0.1 : \mu(x) = \frac{11.8\,x}{1+x} \\
&x \leq 0.1 : \mu(x) = 0
\end{aligned} \qquad [1.28]$$

The equilibrium $x^* = 1.25$ and $y^* = 1.25$ is still unstable. The solution originating from point a meets the line $x = 0.1$ at the point of ordinate a', proceeds along the line and leaves it as soon as it crosses the isocline of the x. Nevertheless, in contrast with the previous case, this trajectory does not return to the line $x = 0.1$. It can be seen that $x(t)$ seems to tend to infinity. In this model, the extractions of the consumer are insufficient to contain the exponential growth of the resource.

1.3.3. *Historical notes and criticisms*

As early as 1934, the Soviet biologist Gause published his experimental results on the Volterra model and drew attention to a book to be published; we will cite the beginning of his argument [GAU 34]:

> "In the last 4 years, I have carried on an experimental investigation of the processes of the struggle for existence among unicellular organisms. Experiments on the competition between two species for a common place in the microcosm agreed completely with Volterra's theoretical equations, but regarding the processes of one species devouring another our results are not concordant with the forecasts of the mathematical theory."

And in the same note, Gause raised awareness about the "atto-fox" phenomenon (although naturally he did not call it so); let us quote him again:

> "This showed that when the number of individuals becomes reduced, and the conditions in the microcosm complicated, instead of the "deterministic" processes subject to differential equations we are confronted with "probabilities of change" in one direction or another. The corresponding material will be found in the above-mentioned book[11]."

In an article in 1936 [GAU 36], Gause and colleagues highlight the existence of refuges:

> "It can be seen that a certain threshold concentration of yeast cells sedimenting on the bottom and elsewhere cannot be destroyed by predators; and predators, even under artificial rarification, do not seriously decrease in concentration until the destruction of the prey down to this threshold (which is partially connected with the decrease in the size of the predators). The threshold has in no way a firmly fixed value, but depends upon the concentration of yeast; when the concentration is high, more cells sediment firmly on the

11 This is referring to [GAU 71].

bottom and escape destruction and the threshold is more pronounced. The escapes due to sedimentation and other causes, and consequently the threshold, intrinsically accompany the interaction between Paramecia and yeast cells.(. . .)

It would be interesting to account for the observed experimental situation theoretically."

They then introduce the model that we have presented, make a mathematical analysis thereof with the resources available at the time (no simulations on computers and no clear concepts of discontinuous right-member differential equations) and provide the very interesting figure that we reproduce in Figure 1.11.

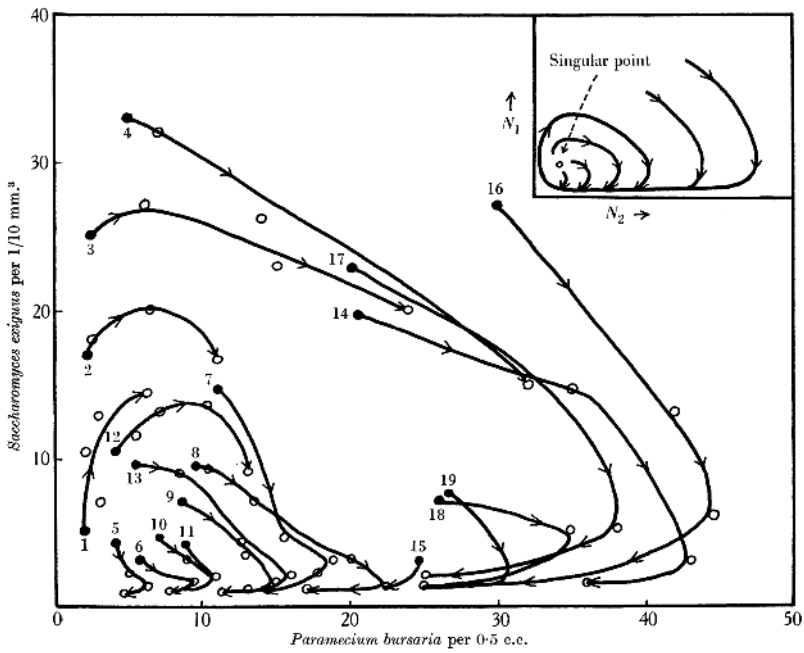

Fig. 4. Interaction between predators (*Paramecium bursaria*) and prey (*Saccharomyces exiguus*).

Figure 1.11. *Excerpt from [GAU 36]*

It should be noted that the roles of x and y are interchanged, consumers are in abscissa and the resource is in ordinate. It can be observed that there is good qualitative agreement between experimental results and the model (inset: the representation of the phase portrait of the model).

Recently, V. Krivan [KŘI 11] has made the effort of performing a rigorous mathematical analysis of this model using tools developed in another context in the early 1960s and has showed that Gause's insights and those of his collaborators were quite correct. Gause's book [GAU 71] is considered to be a classic.

1.4. The Rosenzweig–MacArthur model

1.4.1. *The model*

Whether it is Lotka, Volterra or Gause, all assume that, in the absence of its consumer, the resource increases exponentially without limit. This is an unrealistic assumption: even when no herbivores are present, the amount of grass produced by a territory cannot exceed certain limits. The Rosenzweig–MacArthur model maintains the assumption of bounded nonlinear consumption, overlooks the issue of the threshold introduced by Gause, but adds the assumption that the resource, in the absence of consumer, presents a logistic growth. This yields the model:

$$\begin{aligned}\frac{dx}{dt} &= rx - \alpha x^2 - \frac{\mu_{\max}\, x}{e+x} y \\ \frac{dy}{dt} &= \left(c\frac{\mu_{\max}\, x}{e+x} - m \right) y\end{aligned} \qquad [1.29]$$

The term c measures the yield and, unlike previous cases, we will not seek to remove this term by means of manipulating units. For the simplicity of the calculations that follow, we introduce the notations: $f(x) = rx - \alpha x^2$ and $\mu(x) = \frac{\mu_{\max}\, x}{e+x}$. With these notations, the model becomes:

$$\begin{aligned}\frac{dx}{dt} &= f(x) - \mu(x)\, y \\ \frac{dy}{dt} &= (c\mu(x) - m)\, y\end{aligned} \qquad [1.30]$$

By extension, we will also designate by models of the *Rosenzweig–MacArthur* type, models of the form [1.30] where the functions f and μ are not necessarily quadratic functions for f, or homographic for μ. For example, we could take a Haldane function for μ:

$$\mu(x) = \frac{\mu_{\max}\, x}{e + x + h\, x^2}$$

which takes inhibitory effects into account when the resource is too abundant (when x increases, μ eventually decreases).

1.4.2. *Analysis and simulations*

We proceed with a quick mathematical analysis of this model, a more careful study will be made in Chapter 2.

Isoclines and equilibria.

The isoclines are:

– The isocline of the x: $\frac{dx}{dt} = 0$

$$\left\{(x,y) : y = \frac{f(x)}{\mu(x)} = \frac{(r-\alpha x)(e+x)}{\mu_{\max}}\right\} \bigcup \left\{(x,y) : x = 0\right\}.$$

– The isocline of the y: $\frac{dy}{dt} = 0$

$$\left\{(x,y) : c\mu(x) = c\frac{\mu_{\max}\, x}{e+x} = m\right\} \bigcup \left\{(x,y) : y = 0\right\}.$$

Three possible cases according to the values of m are shown in Figure 1.12:

1) $c\mu_{\max} < m$.

2) $0 < m < c\mu_{\max}$. Let x_2^* be the only x such that $c\mu(x) = m$. We choose m such that the line $x = x_2^*$ cuts the isocline of the x to the right of its peak.

3) $0 < m < c\mu_{\max}$. Let x_3^* be the only x such that $c\mu(x) = m$. We choose m such that the line $x = x_3^*$ cuts the isocline of the x to the left of its peak.

In case 1, there is no equilibrium other than $(0,0)$ and $(r/\alpha, 0)$; in cases 2 and 3, in addition to $(0,0)$ and $(r/\alpha, 0)$, there is an equilibrium (x^*, y^*) defined by the relations:

$$c\mu(x^*) = m \qquad y^* = \frac{f(x^*)}{\mu(x^*)}.$$

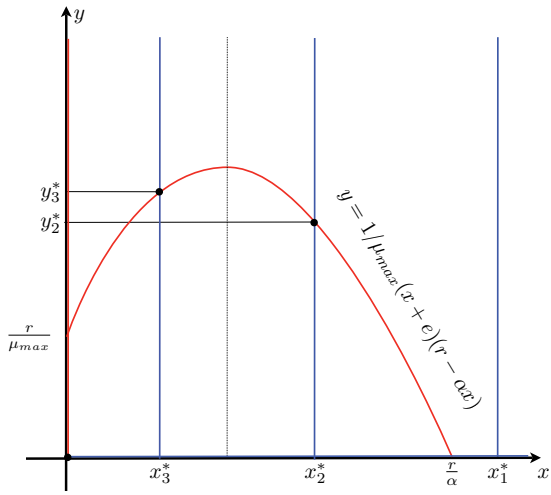

Figure 1.12. *The isoclines of [1.29]. For a color version of this figure, see www.iste.co.uk/lobry/consumer.zip*

In order to analyze the stability of these equilibria, we compute the Jacobian matrix:

– At $(0, 0)$, we have:

$$\begin{pmatrix} f'(x) - \mu'(x)y & -\mu(x) \\ c\mu'(x)y & c\mu(x) - m \end{pmatrix} = \begin{pmatrix} r & 0 \\ 0 & -m \end{pmatrix} \quad [1.31]$$

Therefore, this equilibrium is still unstable.

– At $(r/\alpha, 0)$, we have:

$$\begin{pmatrix} f'(x) - \mu'(x)y & -\mu(x) \\ c\mu'(x)y & c\mu(x) - m \end{pmatrix} = \begin{pmatrix} f'(r/\alpha) & \mu(r/\alpha) \\ 0 & c\mu(r/\alpha) - m \end{pmatrix} \quad [1.32]$$

Here, the stability depends on the sign of $c\mu(r/\alpha) - m$: the equilibrium is stable in case 1 and still unstable in cases 2 and 3.

– At (x^*, y^*), we have:

$$\begin{pmatrix} f'(x^*) - \mu'(x^*)y^* & -m/c \\ c\mu'(x^*)y^* & 0 \end{pmatrix} \quad [1.33]$$

The determinant of this matrix is positive, thereby the stability of the equilibrium depends on the sign $f'(x^*) - \mu'(x^*)y^*$. We have:

$$f'(x^*) - \mu'(x^*)y^* = f'(x^*) - \frac{\mu'(x^*)f(x^*)}{\mu(x^*)} = \mu(x^*)\left(\frac{f}{\mu}\right)'_{x^*}.$$

It can therefore be seen that in case 2 when the line $x = x^*$ cuts the isocline of the x to the right of the top of the isocline, we have $\left(\frac{f}{\mu}\right)'_{x^*} < 0$ and the equilibrium is thus stable; whereas in case 3, the equilibrium is unstable.

Simulations.

– COMMENTS ABOUT FIGURE 1.13.– We have simulated the model:

$$\begin{aligned} \frac{dx}{dt} &= 2x - 2x^2 - \frac{x}{0.1+x}y \\ \frac{dy}{dt} &= \left(c\frac{x}{0.1+x} - m\right)y \end{aligned} \qquad [1.34]$$

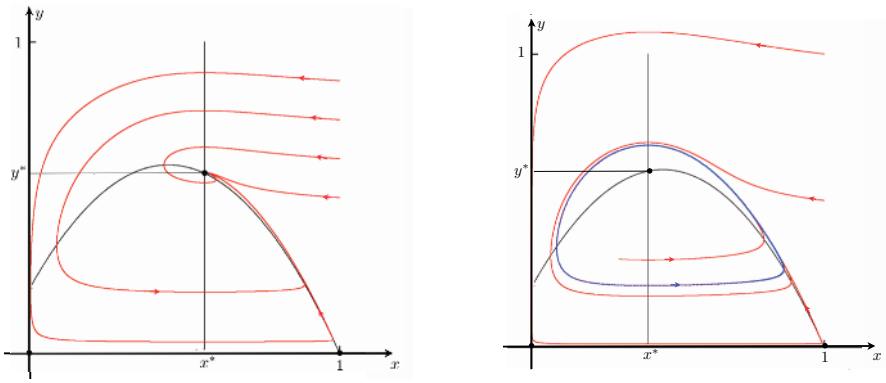

Figure 1.13. *Simulations of [1.29]. Comments in the text. For a color version of this figure, see www.iste.co.uk/lobry/consumer.zip*

For values $c = 1$, $m = 0.85$ (on the left) and $m = 0.75$ (on the right).

- For $m = 0.85$, this corresponds to case 2. The equilibrium (x^*, y^*) can be observed at the intersection of the two isoclines (plotted in black), all trajectories converge to this equilibrium.

- For $m = 0.75$, the isocline has shifted to the left of the top of the parabole which thus corresponds to case 3 where the equilibrium (x^*, y^*) is unstable. The simulation shows the existence of a limit cycle (in blue, in the simulation). We will see how to demonstrate the existence of such cycles in Chapter 2.

COMMENTS ABOUT FIGURE 1.14.– The model [1.29] was simulated with values $m = 0.75$, $c = 0.2$ (on the left) and $c = 0.02$ (on the right). These simulations have highlighted the influence of the parameter c which represents the yield. Again, we are faced with case 3, there is still a limit cycle but this time it *follows along* the vertical axis, as for specific cycles of the Lotka–Volterramodel. In the case in which $c = 0.2$, the minimum achieved by x is $8.24\ 10^{-8}$ which is already small, but for $c = 0.02$, the minimum is $1.6\ 10^{-57}$. Such a model could only be applied to populations of the order of the 10^{60} individuals. This is a problem because, although they are small, yields of 5% are not impossible. In this case, the model does not predict extinction as it should do. We address this problem in Chapter 4.

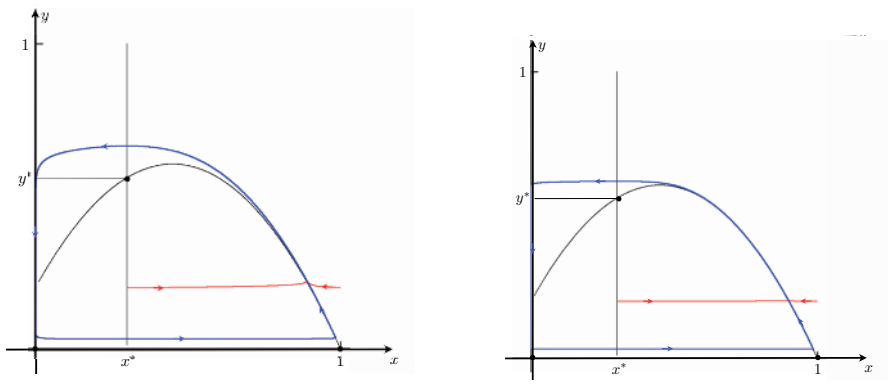

Figure 1.14. *Simulations of [1.29]. Comments in the text. For a color version of this figure, see www.iste.co.uk/lobry/consumer.zip*

1.4.3. *Historical remarks and criticisms*

In his book *Models in Ecology* [MAY 74], J. Maynard Smith attributes to an article by Rosenzweig–MacArthur in 1963 [ROS 63] the paternity of the model [1.29] but he acknowledges that he includes a modified form thereof

(the one that we have presented) in his book. Other authors prefer to refer to Gause to mention this type of model [1.29].

The model [1.29] presents a serious problem that we quickly expose. A *trophic chain* is a sequence of populations, in which each one is the resource of the following one and the consumer of the previous. For example, phytoplankton is consumed by zooplankton which is consumed by (small) fish that are consumed by (bigger) fish, etc. The model below accounts for such a situation.

$$\begin{aligned}
\frac{dx_1}{dt} &= U - \mu_1(x_1)x_2 \\
\frac{dx_2}{dt} &= \mu_1(x_1)x_2 - \mu_2(x_2)x_3 \\
\frac{dx_3}{dt} &= \mu_2(x_2)x_3 - \mu_3(x_3)x_4 \\
\frac{dx_4}{dt} &= \mu_3(x_3)x_4 - mx_4
\end{aligned} \qquad [1.35]$$

The constant U represents a constant supply in resource for consumer 1 that is consumed by population 2, in turn consumed by population 3 which is finally consumed by population 4, which for its part is subject to a disappearance of rate m. All functions μ_i are increasing functions, null at 0, of their argument. Let us determine the equilibrium of such a system, more specifically solve:

$$\begin{aligned}
&(1) \qquad 0 = U - \mu_1(x_1)x_2 \\
&(2) \qquad 0 = \mu_1(x_1)x_2 - \mu_2(x_2)x_3 \\
&(3) \qquad 0 = \mu_2(x_2)x_3 - \mu_3(x_3)x_4 \\
&(4) \qquad 0 = \mu_3(x_3)x_4 - mx_4
\end{aligned} \qquad [1.36]$$

– By adding up the four equations, we obtain: $x_4 = \frac{U}{m}$.

– From (4), we obtain: $\mu_3(x_3) = m$, i.e. $x_3 = \mu_3^{-1}(m)$.

– From (3), we obtain:$\mu_2(x_2)\mu_3^{-1}(m) - \mu_3(x_3)x_4$, i.e. $x_2 = \mu_2^{-1}\left(\frac{U}{\mu_3^{-1}(m)}\right)$.

– And finally, from (1), it follows that: $\mu_1(x_1)\mu_2^{-1}\left(\frac{U}{\mu_3^{-1}(m)}\right) = U$, i.e.:

$$x_1 = \mu_1^{-1}\left(\frac{U}{\mu_2^{-1}\left(\frac{U}{\mu_3^{-1}(m)}\right)}\right).$$

Now, let us look at what happens when U is increased. The equilibrium of level 4 increases in proportion to U while the equilibrium of level 3 *remains constant*. It suffices to replace the μ_i by explicit functions such as $\mu_i(x_i) = \frac{\mu_{max\,i}x}{e_i+x}$ to see that x_2 increases in a nonlinear fashion and finally that x_1 *decreases*. In the table, we summarize:

Trophic level	1	2	3	4
U increasing	↘	↑	→	↗

[1.37]

This response to an increase in primary productivity is certainly awkward and different from what can be observed in reality, where, in general, all levels respond with an increase.

Another criticism that can be made, also valid for all the other models seen so far, is the issue of competitive exclusion. Imagine that two consumers use the same resource. A model derived from [1.30] is:

$$\begin{aligned}\frac{dx}{dt} &= f(x) - \mu_1(x)\,y_1 - \mu_2(x)\,y_2\\ \frac{dy_1}{dt} &= (c_1\mu_1(x) - m_1)\,y_1\\ \frac{dy_2}{dt} &= (c_2\mu_2(x) - m_2)\,y_2\end{aligned} \qquad [1.38]$$

What can be said about the equilibria of this model? To cancel the last two equations without canceling neither y_1 nor y_2, it is simultaneously necessary that we have:

$$c_1\mu_1(x) = m_1 \qquad c_2\mu_2(x) = m_2,$$

which in general is not possible. At equilibrium, we must thus have either $y_1 = 0$ or $y_2 = 0$. One of the two species eliminates the other, this is what is

called *the competitive exclusion principle*. The whole of Chapter 3 will cover this issue. For the moment, we will merely say that if the competitive exclusion principle is sometimes observed, it is far from being a generality. There are situations where a large number of species exist consuming a very small number of resources, in which models similar to the [1.38] type are not able to account for.

1.5. The "ratio-dependent" model

In response to previous criticisms and to others that we have not covered, in 1989 Arditi and Ginzburg [ARD 89] proposed the model:

$$\begin{aligned} \frac{dx}{dt} &= f(x) - \mu(x/y)\, y \\ \frac{dy}{dt} &= (c\mu(x/y) - m)\, y \end{aligned} \qquad [1.39]$$

which is known as the ratio-dependent model or Arditi–Ginzburg ratio-dependent model. In this model, extraction rate and growth rate are not, as in the previous models, functions of only the resource but functions of *the amount of resource available per consumer* which is the quotient "x/y".

1.5.1. *Model analysis and simulations*

We consider the model [1.39] with:

$$f(x) = rx - \alpha x^2 \qquad \mu(y/x) = \frac{\mu_{\max} x/y}{e + x/y} = \frac{\mu_{\max} x}{ey + x} \qquad [1.40]$$

1.5.1.1. *Isoclines and equilibria*

The first difference with all previous models in which the isocline of the y was the vertical line $x = x^*$ where x^* is the solution, when it exists, of the equation $c\mu(x) = m$, is now the line going through the origin defined by $c\mu(x/y) = m$. This form of the isocline of y changes a lot of things.

The isocline of the x is now implicitly defined by:

$$f(x) - \mu(x/y)\, y = 0 \qquad [1.41]$$

and no longer as a graph by $y = \frac{f(x)}{\mu(x)}$ which can make its analysis more complicated. In the case of the choice that we have made [1.40], after an easy computation, the isocline of the x is defined by:

$$\left\{(x,y) : y = \frac{rx - \alpha x^2}{(\mu_{\max} - e\,r) + er\,\alpha x}\right\} \bigcup \left\{(x,y) : x = 0\right\} \qquad [1.42]$$

The form of this isocline will essentially depend on the sign of $(\mu_{\max} - e\,r)$.

We will cover the computation of equilibria and their stability in detail in Chapter 2.

1.5.1.2. *Trophic chain response*

We continue this analysis by observing what happens in a four-level trophic chain. We reconsider the system [1.35] but with $\mu_i(x_i/x_{i+1})$ instead of $\mu_i(x_i)$. To determine the equilibrium, it is necessary to solve:

$$\begin{aligned}
&(1) \quad 0 = U - \mu_1(x_1/x_2)x_2 \\
&(2) \quad 0 = \mu_1(x_1/x_2)x_2 - \mu_2(x_2/x_3)x_3 \\
&(3) \quad 0 = \mu_2(x_2/x_3)x_3 - \mu_3(x_3/x_4)x_4 \\
&(4) \quad 0 = \mu_3(x_3/x_4)x_4 - mx_4
\end{aligned} \qquad [1.43]$$

– By adding up the four equations, we obtain: $x_4 = \frac{U}{m}$.

– From (4), we obtain: $\mu_3(x_3/x_4) = m$, i.e.:
$x_3 = x_4\mu_3^{-1}(m) = \frac{U}{m}\mu_3^{-1}(m)$, which is an increasing function of U.

– From (3)+(4), we obtain: $\mu_2(x_2/x_3) = mx_4 = U$, i.e. $x_2 = x_3\mu_2^{-1}(U)$, which is an increasing function of U since that is the case of x_3.

– Finally, from (2)+(3)+(4), we can extract: $\mu_1(x_1/x_2) = mx_4 = U$, i.e. $x_1 = x_2\mu_1^{-1}(U)$, which is an increasing function of U since this is the case of x_2.

Therefore, at any level of the trophic chain, the equilibrium responds in a increasing manner to an increase in the primary resource U, which is much more satisfying than what was occurring in the "resource-dependent case".

1.5.1.3. *Simulations*

COMMENTS ABOUT FIGURE 1.15.– It can be observed that this figure shows the results of a simulation of [1.39] for functions f and μ defined by [1.40] and for the values of the parameters indicated in table [1.44]. In the simulation on the left the two isoclines (in black) and the equilibrium (x^*, y^*) that they define can be observed. This equilibrium is asymptotically stable but not globally. Its basin of attraction has been colored in yellow. In light green, we have all the trajectories that tend toward $(0, 0)$. In the simulation on the right side, all the parameters are identical except the disappearance term which is smaller. The equilibrium continues to be stable and is surrounded by a stable limit cycle (in blue). As in the previous case, the basin of attraction (in yellow) of the limit cycle is not the whole orthant.

	c	r	α	$\mu_{\max}$	e	m
left	1	2	2	1	0.2	0.85
right	1	2	2	1	0.2	0.7485

[1.44]

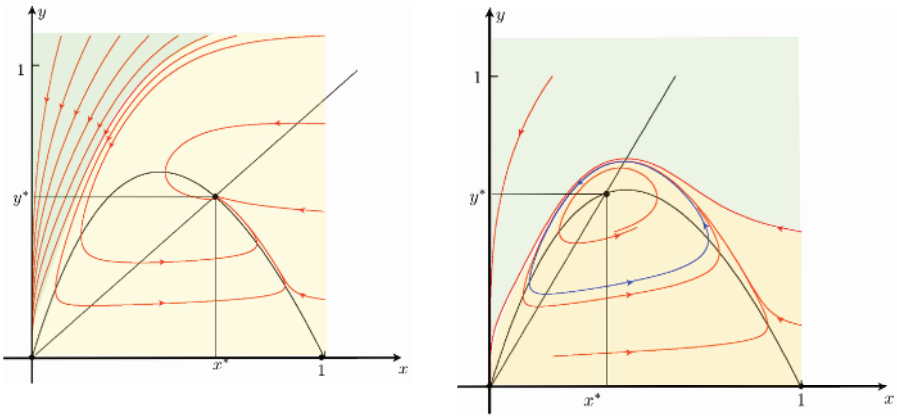

Figure 1.15. *Simulations of [1.39]. Comments in the text. For a color version of this figure, see www.iste.co.uk/lobry/consumer.zip*

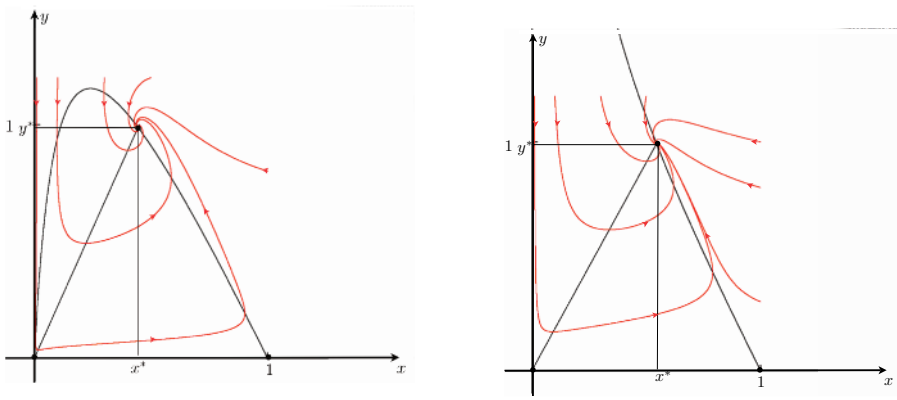

Figure 1.16. *Simulations of [1.39]. Comments in the text. For a color version of this figure, see www.iste.co.uk/lobry/consumer.zip*

COMMENTS ABOUT FIGURE 1.16.– In this figure, the model [1.39] has been simulated with the functions f and μ defined by [1.40] and with more significant values of e than in the previous case.

	c	r	α	$\mu_{\max}$	e	m
left	1	2	2	1	0.45	0.5
right	1	2	2	1	0.55	0.5

[1.45]

It can be seen that the form of the isocline of the x completely changes and that now equilibria appear to be globally stable.

All these simulations will be analyzed in detail in Chapter 2.

1.5.2. *Historical notes and criticisms*

Proposals had already been made before Arditi–Ginzburg to "improve" the Rosenzweig–MacArthur model. For example, Bedington and De Angelis [BED 75, DEA 75] have proposed to take:

$$\mu(x, y) = \frac{\mu_{\max} x}{ey + x + \delta} \qquad [1.46]$$

where it can be seen that μ is not only a function of x but also of y. The term $e\,y$, which decreases the functional response when y increases, is here to

confirm the interference of consumers at high densities. For $\delta = 0$, we recover the ratio-dependent model that we have just simulated. The "mathematical" advantage in taking δ non-zero is that the model is correctly defined at $(0, 0)$ which is not the case for the ratio-dependent model. This specificity, which implies slightly more delicate mathematical analysis, was put forward by the criticisms of "ratio-dependency" during the long controversy that followed the publication of the Arditi–Ginzburg article. We will go back to these issues in Chapter 2.

1.6. Conclusion

Since the original Lotka–Volterra, and in the span of one century, the mathematical model of the consumer–resource relationship has become more complex. This development was motivated since the 1930s by virtue of taking into account experimental data and observations of natural environments that were accumulating, but was slowed down by the need to work within the framework of the mathematical knowledge of the time. From the 1950s onward, new mathematical tools and *especially* computers have become available. With their help, we have been able to address the problems of the consumer–resource relationship in all its generality as desirable. This is what was achieved by a large number of works that we will not attempt to describe further in this introductory chapter.

The next chapter will essentially be dedicated to the mathematical study of both Rosenzweig–MacArthur's model, and that of Arditi–Ginzburg.