



Theoretical investigation of the dependence of population parameters on initial population size

Jean-Pierre Gabriel^a, Louis-Félix Bersier^{b,*}

^a Department of Mathematics, University of Fribourg, Chemin du Musée 23, 1700 Fribourg, Switzerland

^b Department of Biology, University of Fribourg, Chemin du Musée 10, 1700 Fribourg, Switzerland

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ABSTRACT

In a series of experiments with yeast, classical dynamical models were fitted to populations that differed only in their initial population size (Pylvänäinen 2005). The results revealed a surprising dependence between estimated growth rate and initial population size. Perceived as an artefact, this undesired relationship was tentatively removed by an ad-hoc procedure. This strategy reflects the usual approach of population models in which parameters are not considered to depend on initial conditions. However, our analysis reveals that the observed relationship between estimated growth rate and initial population size is unavoidable when the dimension of a system is reduced. For the present case, the two-dimensional food-yeast system was reduced to a model for yeast only. The consequence of system reduction questions our conception of one-dimensional population models.

1. Introduction

The use of one-dimensional population models has a long tradition in ecology and evolutionary biology. Such continuous time models have usually the form $\frac{dN(t)}{dt} = f(N(t))$, where $N(t)$ is the population size at time t and f is a given function. The parameters involved in f are expected to depend on the environment and the species considered, but not on the initial population size. They are usually estimated by fitting the solution of the model to a single observed trajectory and thus a single initial condition for the population. In the work of Pylvänäinen (2005), growth parameters were estimated by fitting the trajectories of numerous replications of the same strain of yeast in strictly controlled experimental conditions. A very interesting and unusual feature of this research was the use of different initial population sizes $N(0)$, which were measured but not fitted. The dynamical parameters were estimated for several one-dimensional models. Surprisingly, the fitted parameters turned out to depend on the initial population size (Fig. 1). Perceived as an artefact, this dependence was removed by introducing a new model where the growth curve was segmented into three parts (an intermediate Malthusian phase flanked by two segments obeying a Chapman-Richards growth function), and standardising the central exponential segment. This approach is coherent with the classical theory of population models in which parameters do not depend on the initial population size.

What could be the source of the observed dependence between the fitted parameters and the initial conditions? Several causes may underly such a dependence, for example the use of an inadequate

model (see Appendix A), measurement errors, uncontrolled factors in the experiment... In the absolute, one cannot escape the problems of measurement errors and of model correctness. As a consequence, the presence of this dependence is a priori not surprising. However, even in the ideal case of a perfect model and observations without errors, we will show that this dependence is unavoidable for one-dimensional population models, and more generally for any dynamical system in reduced dimension.

We start with two resource-consumer models, the batch and the chemostat, that can be reduced to a one-dimensional consumer model with a logistic shape. In this way, we can identify the classical parameters r , the intrinsic growth rate, and K , the non-trivial equilibrium population size. We then show that the appearance of the initial conditions is a general consequence of model reduction for any system of coupled differential equations.

2. Results

2.1. System reduction in a batch culture

The dynamics of a population always involves several external factors (nutrients, competitors, predators...) requiring a system of several coupled equations for its description. Let us consider a simple case, namely the growth of a microorganism in a batch culture with only one nutrient. A batch culture is a closed fermentor where inert food is provided at the beginning, as was the case in the yeast

* Corresponding author.

E-mail address: louis-felix.bersier@unifr.ch (L.-F. Bersier).

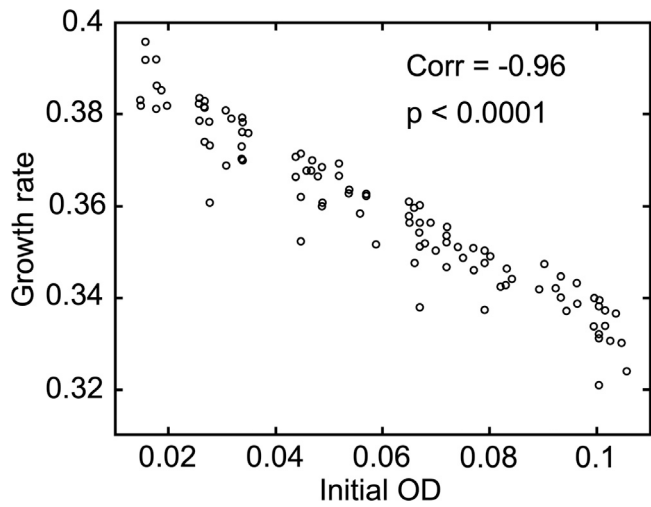


Fig. 1. Parameter dependence. Relationship between initial population size (measured as OD, Optical Density) and estimated *maximum relative growth rate* from the Chapman-Richards model for 99 wild type populations of *Saccharomyces cerevisiae* grown in batch culture conditions. The experiment was simultaneous for the 99 wild types, and OD-values were blank corrected and calibrated. ‘Corr’ is Pearson correlation coefficient with the associated *p*-value.
Source: Redrawn from Fig. 3.8 in Pylvänäinen (2005).

studies (Pylvänäinen, 2005). Assuming that food is used only for reproduction and that mortality and metabolic costs are neglected, the equations for the population size $N(t)$ and the food concentration $X(t)$ obey the following system of equations:

$$\begin{aligned} \frac{dN(t)}{dt} &= \frac{1}{\theta} h(X(t)) N(t), \\ \frac{dX(t)}{dt} &= -h(X(t)) N(t), \end{aligned} \quad (1)$$

where θ is a conversion factor expressing the quantity of food necessary to produce one microorganism, and h is the food consumption function per unit of time and per microorganism. It is mathematically easy to reduce this multidimensional system to a one-dimensional equation for the microorganism. Indeed, the equations entail $\theta \frac{dN(t)}{dt} + \frac{dX(t)}{dt} = \frac{d}{dt}(\theta N(t) + X(t)) = 0$, and thus $\theta N(t) + X(t) = \text{constant} = \theta N(0) + X(0)$, reflecting matter conservation. Since $X(t) = \theta N(0) + X(0) - \theta N(t)$, we deduce the following equation for $N(t)$:

$$\frac{dN(t)}{dt} = \frac{1}{\theta} h(\theta N(0) + X(0) - \theta N(t)) N(t). \quad (2)$$

Following McKendrick and Pai (1911), we assume the consumption function h to be proportional to the food concentration, i.e. $h(X) = \alpha X$, where α is the food consumption rate per microorganism. This leads to:

$$\frac{dN(t)}{dt} = \alpha \left[N(0) + \frac{1}{\theta} X(0) \right] N(t) - \alpha N^2(t). \quad (3)$$

Hence, the initial conditions $N(0)$ and $X(0)$ appear in the differential Eq. (3). The reduced equation contains $X(0)$, which is not surprising as it represents the state of the environment at the start of the experiment. The presence of $N(0)$ in the reduced equation is however remarkable. In the standard case, $N(0)$ appears only in its solution. Eq. (3) has a logistic form and it is then possible to identify the classical ecological parameters r and K . It turns out that both depends on $N(0)$ and $X(0)$: $r = \alpha \left[N(0) + \frac{1}{\theta} X(0) \right]$ and $K = N(0) + \frac{1}{\theta} X(0)$ (see Fig. 2).

It is worth comparing our Eq. (3) with the one of McKendrick and Pai (1911). As mentioned, they proposed a model for the batch system and suggested that the per capita rate of multiplication is proportional to the ‘food-stuff’. Food concentration at time t was proposed to be $X(t) = X(0) - N(t)$; this implies that our parameter θ equals 1 in their

case. The resulting equation is the following:

$$\frac{dN(t)}{dt} = \alpha X(0) N(t) - \alpha N^2(t). \quad (4)$$

This is a logistic model with $r = \alpha X(0)$ and $K = X(0)$. However, since the initial amount of food equals the food at time t plus the food used to build the microorganisms between time 0 and time t , we have $X(0) = X(t) + (N(t) - N(0))$ or $X(t) = X(0) - N(t) + N(0)$.

The batch model as proposed here has strong assumptions, notably the absence of mortality. We can explore the consequences of adding a mortality term μ to Eq. (1). Assuming that the dead organisms do not participate to the dynamics (no recycling, no toxic effects...), the new equation reads:

$$\begin{aligned} \frac{dN(t)}{dt} &= \frac{1}{\theta} h(X(t)) N(t) - \mu N(t), \\ \frac{dX(t)}{dt} &= -h(X(t)) N(t). \end{aligned} \quad (5)$$

Using again a linear function for food consumption, the reduced equation for the population of microorganisms is now :

$$\frac{dN(t)}{dt} = \alpha \left[X(0) + \theta N(0) - \theta N(t) - \theta \int_0^t \mu N(s) ds \right] N(t) - \mu N(t). \quad (6)$$

We observe that the initial condition $N(0)$ remains in the reduced model, which is now an integro-differential equation that does not anymore have a logistic shape: after having reached a maximum, the population decreases to an equilibrium density equal to 0 (see Appendix B for derivation).

This first exploration of the consequences of system reduction is based on the batch culture, which is a closed system where the resource is monotonically decreasing toward 0. This hardly corresponds to any natural system and one may wonder if the presence of initial conditions in the reduced differential Eq. (3) only happens in the special case of closed systems. A chemostat is a constant-volume fermentor with continuous food input and effluent output. This system better corresponds to natural ones since the resource has its own dynamics (though admittedly a very simple one) and the outflow can be seen as a form of mortality for the microorganism. In the Appendix C, we reduce the system of equations for the chemostat to a single equation for the microorganism, and show how it can be tuned to yield a logistic form. Again, the ecological parameters r and K appear to depend on the initial population size $N(0)$.

2.2. System reduction in a general context

For simplicity, we consider a system with one species of interest N that interacts with a resource X . A very general autonomous (i.e., time does not appear explicitly in the right-hand side of the equation) model for this system is:

$$\begin{aligned} \frac{dN(t)}{dt} &= f(N, X), \\ \frac{dX(t)}{dt} &= g(N, X), \end{aligned} \quad (7)$$

with f and g functions describing the dynamics of the system. According to the general theory of ordinary differential equations, if the system (7) admits a solution, then:

$$X(t) = h(N(0), X(0), t), \quad (8)$$

for some function h , and then,

$$\frac{dN(t)}{dt} = f\left(N, h(N(0), X(0), t)\right). \quad (9)$$

This simple derivation shows that reducing this system to one equation for the population N entails the presence of $X(0)$, $N(0)$ and t in the right-hand side. Again, it is not surprising that the initial amount of resource $X(0)$ influences the population dynamics, as it represents the environment, but it is striking to note that $N(0)$ also plays this role. Consequently, we can expect that the parameters of a model built

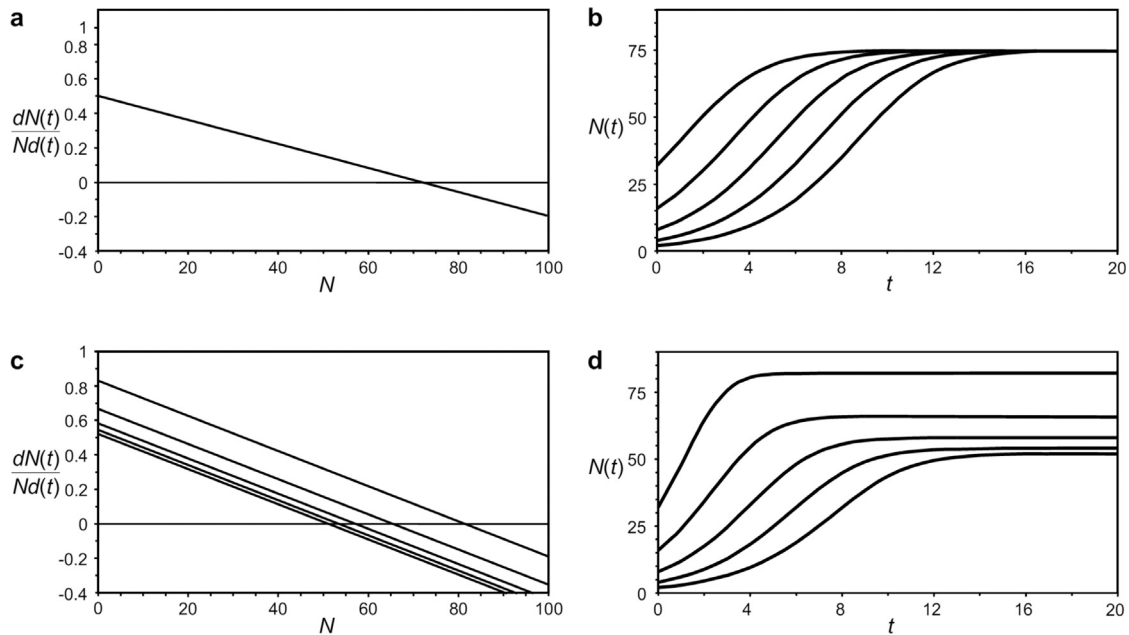


Fig. 2. Comparison of the classical- and the reduced-logistic equation. Per capita rate of increase $dN(t)/Nd(t)$ (a & c) and population size $N(t)$ (b & d) for the classical logistic equation ((a & b); parameters: $r = 0.5$; $K = 75$) and for a logistic derived by reducing the food-population system in a batch culture to one dimension for the population ((c & d); Eq. (3) with parameters $\alpha = 0.01$; $\theta = 10$; $X(0) = 500$; $N(0) = 2, 4, 8, 16,$ and 32 , corresponding to lines from bottom to top).

solely for $N(t)$ will depend on $N(0)$. Moreover, we started with an autonomous system and end up with a non-autonomous one-dimensional equation. Since all ecological systems require resource to survive and develop, and therefore their phase space is at least two-dimensional, we deem these considerations very general. We extend this reasoning to general systems of ordinary differential equations, biological or not, in Appendix D.

3. Discussion

We present evidence that the estimates of classical population parameters are influenced by initial population size in one-dimensional models and, more generally, that reducing a system of ordinary differential equations to lower dimensions entails the intrusion of initial conditions into the model. Our finding has obvious consequences for parameter estimation, for example when studying temperature performance curves (see e.g. Rezende and Bozinovic, 2019). Although a one-dimensional model can provide an excellent fit to a single observed trajectory, changing the initial population size will generally lead to different parameter estimates.

In our investigation, the reduced batch equation had a logistic form, and we showed how to tune the reduced chemostat equation to exhibit a logistic shape. This allowed the identification of two fundamental parameters of population ecology, namely the intrinsic growth rate r and the equilibrium density K . Does the dependence to initial conditions only happen for these particular parameters? In the unusual work of Pylvänäinen (2005), three ‘physiologically important parameters’ were estimated. First, as shown in Fig. 1, the ‘maximum relative growth rate’ depended on initial optical density (OD); it was measured as the maximum derivative of the log-transformed growth curve and is thus different from the r of the logistic equation. Second, the ‘lag time’ is the duration of the lag phase typically observed in the growth of microorganisms. Interestingly, this parameter was also found to depend on the initial OD. Third, the ‘stationary phase OD increment’ is a measure of population size at equilibrium. It was measured as the final OD minus the initial OD and did not depend on initial OD. This is exactly what we would expect since the stationary phase OD increment equals K minus $N(0)$. Consequently, as suggested from the reduction of a system in the general context, we can expect that the estimation

of any parameter of a reduced model can be affected by the initial conditions.

Practically, when population parameters have to be estimated experimentally with one-dimensional models, standardising the initial population size to low values is a sensible solution to avoid strong bias. For the yeast system in Fig. 1, a 10 times increase of $N(0)$ (from 0.01 to 0.1 OD) induced a decrease of the estimated growth rate by roughly 15%. Interestingly, since this relationship here is linear, it would be straightforward to estimate the growth rate at $N(0) = 0$. Such approaches are promising and should be explored in more depth. However, they require multiple cultures with different $N(0)$. Finally, note that the parameters of the non-reduced equations should not be affected by the initial conditions, but their estimation would generally require to follow the dynamics of all actors of the system.

There are specific consequences of model reduction that are worth mentioning. First, in the batch situation without mortality (Eq. (3)), the parameter K is equal to the total number of organisms obtained by food conversion plus the initial number $N(0)$. This implies that $N(0)$ and K are linked in a way that $N(0)$ never exceeds K . Second, it is well known that the parameters r and K are not independent of each other in the logistic equation. Verhulst (1838) original formulation of the logistic model does not include the parameter K , but a ‘friction’ term n that is now interpreted as intraspecific competition ($\frac{dN(t)}{dt} = rN - nN^2$, with $K = \frac{r}{n}$). This parameter n is assumed to be independent of r . This is however not the case in the reduced batch and chemostat equations. Here, we can identify n with the per capita food consumption rate α , which is also present in the definitions of r . Third, adding a linear mortality term $-\mu N(t)$ in the batch system (Eq. (5)) has a non-trivial consequence: in this case, the form of the reduced equation is not logistic anymore and $N(\infty) = 0$. Interestingly, adding this linear mortality term into the traditional logistic equation will not change its form and the new equilibrium density is $N(\infty) = (r - \mu)/n$ (Ginzburg, 1992; Gabriel et al., 2004). Fourth, as discovered for the chemostat, one can expect in general the reduced equation to be non-autonomous. This feature might notably complicate the analysis. Fifth, in usual classical differential equations, two trajectories with different initial conditions can never cross in a finite time (uniqueness of the solutions). This property can get lost when $N(0)$ appears in the equation (see Appendix E for an example). One can visualise the problem of model reduction by

considering the phase space of a multidimensional system of ordinary differential equations. The trajectories of the system never cross in the full dimensional phase space. The paths of a reduced equation are their projections on a subset in lower dimensional space and, in general, this projection does not preserve the unicity property. Note that this situation does not happen in the above batch and chemostat reduced equations.

4. Conclusion

Our finding questions the use of one-dimensional models to estimate population-growth parameters. A multi-dimensional approach of population dynamics for parameter estimation would clearly be an improvement. However, it requires the characterisation of the key interacting factors that participate to the dynamics of the species of interest, and to monitor their time evolution. In all, our contribution asks for a critical reconsideration of the principles underlying one-dimensional population models.

CRediT authorship contribution statement

Jean-Pierre Gabriel: Conceptualization, Writing, Mathematical developments. **Louis-Félix Bersier:** Conceptualization, Writing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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Appendix A. Fitting an inadequate model

Let us consider a Malthusian population whose size is given by $n(t) = n(0)e^{at}$ for $t \geq 0$. We shall try to fit an affine function $x(t) = at + b$ to represent the preceding function. The observation of the population at times $0 < t_1 < t_2 < \dots < t_n$ provides the data $n(t_1), n(t_2), \dots, n(t_n)$ and we estimate a and b with the least square method. We thus deal with the following system:

$$\begin{aligned} at_1 + b &= n(0)e^{at_1} \\ at_2 + b &= n(0)e^{at_2} \\ &\dots \\ at_n + b &= n(0)e^{at_n} \end{aligned} \tag{A.1}$$

whose vectorial form is

$$A\underline{X} = \underline{B} \tag{A.2}$$

where

$$A = \begin{bmatrix} t_1 & 1 \\ t_2 & 1 \\ \vdots & \vdots \\ t_n & 1 \end{bmatrix}, \quad \underline{X} = \begin{bmatrix} a \\ b \end{bmatrix}, \quad \underline{B} = \begin{bmatrix} n(0)e^{at_1} \\ n(0)e^{at_2} \\ \vdots \\ n(0)e^{at_n} \end{bmatrix}.$$

Let A^T be the transpose of A . Since the rank of A is 2 the matrix $A^T A$ is invertible and the least square solution \underline{X}_{ls} is given by

$$\underline{X}_{ls} = (A^T A)^{-1} A^T \underline{B} = n(0)(A^T A)^{-1} A^T \begin{bmatrix} e^{at_1} \\ e^{at_2} \\ \vdots \\ e^{at_n} \end{bmatrix}. \tag{A.3}$$

The initial condition $n(0)$ cannot be canceled unless $(A^T A)^{-1} A^T \begin{bmatrix} e^{at_1} \\ e^{at_2} \\ \vdots \\ e^{at_n} \end{bmatrix}$

is the zero-vector. Since $A^T \begin{bmatrix} e^{at_1} \\ e^{at_2} \\ \vdots \\ e^{at_n} \end{bmatrix}$ is a non-zero vector and $(A^T A)^{-1}$ is invertible, at least one of the two parameters a or b depends on $n(0)$.

Appendix B. Mortality in the batch model

The system of differential equations for the batch system with mortality is given by :

$$\begin{aligned} \frac{dN(t)}{dt} &= \frac{1}{\theta} f(X(t))N(t) - \mu N(t), \\ \frac{dX(t)}{dt} &= -f(X(t))N(t), \end{aligned} \tag{B.1}$$

with $N(t)$ the size of the population, $X(t)$ the food concentration, θ the amount of food necessary to produce one microorganism, f the food-consumption function, and μ the mortality rate. The function f is assumed to be continuously differentiable over \mathbb{R}^+ with a unique zero for $X = 0$. Since $f(0) = 0$, the preceding assumption entails the continuity of $g(X) = \frac{f(X)}{X}$ over \mathbb{R}^+ . The general theory of ode's provides the existence and unicity of a local solution for any initial condition $N(0) > 0$ and $X(0) > 0$. This solution, defined over a maximal right-hand interval J^+ , satisfies:

$$\begin{aligned} N(t) &= N(0)e^{\int_0^t (\frac{1}{\theta} f(X(s)) - \mu) ds}, \\ X(t) &= X(0)e^{-\int_0^t g(X(s))N(s) ds}. \end{aligned} \tag{B.2}$$

As a consequence, $N(t)$ and $X(t)$ are strictly positive over J^+ . Moreover we have $\theta \frac{dN(t)}{dt} + \frac{dX(t)}{dt} = -\theta \mu N(t) < 0$ showing that $\theta N(t) + X(t)$ is decreasing over J^+ . Since it is positive, it has to be bounded and thus N and X have the same property entailing the existence and uniqueness of the solution over \mathbb{R}^+ . The function X is decreasing and thus admits a limit X_∞ as $t \rightarrow +\infty$. Since $\theta \frac{dN(t)}{dt} + \frac{dX(t)}{dt}$ has the same property, N also has a limit N_∞ . According to our system, $\frac{dN(t)}{dt}$ and $\frac{dX(t)}{dt}$ converge and thus converge to 0 as $t \rightarrow +\infty$. From $\theta \frac{dN(t)}{dt} + \frac{dX(t)}{dt} = -\theta \mu N(t)$ we deduce that $N_\infty = 0$.

According to the hypotheses of the batch situation, the food quantity removed from the system between times 0 and t is given by $\theta \int_0^t \mu N(s) ds$ and the new equation is

$$\frac{dN(t)}{dt} = \alpha \left[X(0) + \theta N(0) - \theta N(t) - \theta \int_0^t \mu N(s) ds \right] N(t) - \mu N(t). \tag{B.3}$$

with initial condition $N(0) \geq 0$. We can rewrite it as

$$\frac{dN(t)}{dt} = (A - BN(t) - C \int_0^t N(s) ds) N(t), \tag{B.4}$$

with the constants $A = -\mu + \alpha X(0) + \alpha \theta N(0)$, $B = \alpha \theta$, and $C = \alpha \theta \mu$.

The latter is equivalent to the system :

$$\Sigma : \begin{cases} \frac{dN(t)}{dt} = (A - BN(t) - CY(t)) N(t), \\ \frac{dY(t)}{dt} = N(t), \end{cases} \tag{B.5}$$

with initial condition $N(0) > 0$ and $Y(0) = 0$. The local Lipschitz-continuity of the right-hand member of Σ in \mathbb{R}_+^2 provides the existence

and uniqueness of a solution defined over a maximal right-hand interval J^+ . For every $t \in J^+$, the first equation of Σ entails $N(t) = N(0)e^{\int_0^t (A - BN(s) - CY(s)) ds}$ and thus $N(t) > 0$ and $Y(t) > 0$ for $t > 0$ in J^+ . As a consequence $Y(t)$ is increasing over J^+ and the solution cannot reach the boundary of \mathbb{R}_+^2 in a finite time. Moreover $N(t)$ is bounded since its derivative is negative for sufficiently large values of N . As a consequence, $Y(t)$ is bounded over compact intervals and the solution cannot reach $+\infty$ in a finite time. The general theory of ode's provides then the existence of a solution defined over \mathbb{R}_+ . Local unicity implies global unicity. Σ is not a monotone system and it is thus pertinent to study the asymptotic behaviour of $N(t)$.

If, as $t \rightarrow +\infty$, $Y(t) = \int_0^t N(s) ds \uparrow +\infty$, then because of the boundedness of $N(t)$, $A - BN(t) - CY(t) \rightarrow -\infty$ and thus $N(t) = e^{\int_0^t (A - BN(s) - CY(s)) ds} \rightarrow 0$. If, otherwise, $\int_0^t N(s) ds$ is bounded for $t \in \mathbb{R}_+$, then again $N(t) \rightarrow 0$ as $t \rightarrow +\infty$ since, in that case, $\frac{dN}{dt}$ is bounded. Consequently we proved that $\lim_{t \rightarrow +\infty} N(t) = 0$, meaning ultimate extinction of the population, a result consistent with intuition under the assumption that the resource in dead organisms is not recycled. Another consequence is that this model has not anymore a logistic form, which can be proven as follows. The modified equation is:

$$\frac{dN(t)}{dt} = \alpha \left[X(0) + \theta N(0) - \frac{\mu}{\alpha} - \theta N(t) - \theta \int_0^t \mu N(s) ds \right] N(t) \quad (B.6)$$

and, obviously, the latter is a logistic equation if and only if $\int_0^t N(s) ds$ is a polynomial of degree 1 in $N(t)$, i.e. $\int_0^t N(s) ds = DN(t) + E$. This is equivalent to $D \frac{dN(t)}{dt} = N(t)$. If $D = 0$, then $N \equiv 0$. We can therefore assume $D \neq 0$ and thus $N(t) = N(0)e^{Dt-1}$ for all $t \geq 0$. Note that we also assume no recycling of the dead microorganisms in the batch model. Adding a linear recycling term would not change our conclusions, either in Eq. (1) or in Eq. (B.1).

Appendix C. System reduction in the chemostat

A chemostat is a constant-volume fermentor with continuous food input and effluent output. This system can be described by:

$$\begin{aligned} \frac{dN(t)}{dt} &= \frac{1}{\theta} h(X(t))N(t) - qN(t), \\ \frac{dX(t)}{dt} &= q[x_e - X(t)] - h(X(t))N(t), \end{aligned} \quad (C.1)$$

where $N(t)$, $X(t)$, θ , and h have the same meaning as before, x_e is the input concentration, and q is the washout rate divided by V , the volume of the system (Segel, 1984). The system of Eqs. (C.1) implies:

$$\frac{d(\theta N(t) + X(t))}{dt} = -q[\theta N(t) + X(t)] + qx_e \quad (C.2)$$

and thus we have:

$$X(t) = (\theta N(0) + X(0) - x_e)e^{-qt} + x_e - \theta N(t). \quad (C.3)$$

By introducing this relation into the first member of Eq. (C.1), we obtain:

$$\frac{dN(t)}{dt} = \frac{1}{\theta} h \left((\theta N(0) + X(0) - x_e)e^{-qt} + x_e - \theta N(t) \right) N(t) - qN(t). \quad (C.4)$$

The right-hand member of Eq. (C.4) again depends explicitly on the initial population size $N(0)$. Additionally, the latter is now *non-autonomous* since time appears explicitly in the factor e^{-qt} . The system is influenced by an external clock, whose effect vanishes with time.

The reduced batch Eq. (4) has a logistic form, which allows the identification of the parameters r and K that turn out to depend on the initial conditions. Are there situations in the reduced chemostat Eq. (C.4) where $N(t)$ also satisfies a logistic form? For the linear case $h(x) = \alpha x$, we have:

$$\frac{dN(t)}{dt} = \left(\frac{\alpha}{\theta} [(\theta N(0) + X(0) - x_e)e^{-qt} + x_e - \theta N(t)] - q \right) N(t) \quad (C.5)$$

(interestingly, Eq. (C.5) is present in Kostitzin (1956)). In the highly particular case $\theta N(0) + X(0) - x_e = 0$, the preceding equation turns

out to be logistic. However, this form gets lost by changing the initial condition. There is a more robust way to produce a logistic equation: firstly, food is not allowed to leave the system, which is achieved by re-injecting the food part of the outflow (the term $-qX(t)$ cancels out in Eq. (C.1)); secondly, the food input concentration is controlled so that $x_e = x_e(t) = \theta N(t)$. We thus obtain:

$$\begin{aligned} \frac{dN(t)}{dt} &= \frac{1}{\theta} h(X(t))N(t) - qN(t), \\ \frac{dX(t)}{dt} &= q\theta N(t) - h(X(t))N(t). \end{aligned} \quad (C.6)$$

Multiplying the first term of Eq. (C.6) by θ and summing both terms gives $\frac{d}{dt}(\theta N(t) + X(t)) = 0$, and hence $\theta N(t) + X(t) = \theta N(0) + X(0)$ for all $t \geq 0$. Assuming again the linearity of h , we get the logistic equation

$$\frac{dN(t)}{dt} = \left(\alpha N(0) + \frac{\alpha}{\theta} X(0) - q \right) N(t) - \alpha N^2(t). \quad (C.7)$$

Its ecological parameters again depend on $N(0)$: $r = \alpha \left[N(0) + \frac{1}{\theta} X(0) - \frac{q}{\alpha} \right]$ and $K = N(0) + \frac{1}{\theta} X(0) - \frac{q}{\alpha}$. If q is large enough, r and K are negative and all solutions converge to 0 as time goes to infinity. Depending on the values of α, θ, q and $X(0)$, K is either larger or smaller than $N(0)$.

Appendix D. Reduction in systems of dimension > 2

Here, we consider system reduction in a general context. Any species is usually engaged in a constellation of interactions with other species and resources that vary with time, and thus one can expect the number of equations in the system to be large and difficult to identify exhaustively. However, we can easily give a general mathematical form to the problem. We introduce the variables $N(t)$ for the size of the population of interest at time t , and $X_1(t), \dots, X_m(t)$ for the size of the m variables (resource or other species) involved in the dynamical evolution of $N(t)$. In an autonomous situation, the general differential system has the form:

$$\begin{aligned} \frac{dN(t)}{dt} &= f(N(t), X_1(t), \dots, X_m(t)), \\ \frac{dX_1(t)}{dt} &= g_1(N(t), X_1(t), \dots, X_m(t)), \\ &\dots \\ \frac{dX_m(t)}{dt} &= g_m(N(t), X_1(t), \dots, X_m(t)), \end{aligned} \quad (D.1)$$

where f, g_1, \dots, g_m are given functions. The key question is now: can we deduce such an equation for $N(t)$ from the general system? For every initial condition $(N(0), X_1(0), \dots, X_m(0))$, assuming the existence and unicity of a solution defined for all $t \geq 0$, the general theory of ordinary differential equations gives the form of its solution:

$$\begin{aligned} N(t) &= h(N(0), X_1(0), \dots, X_m(0), t), \\ X_1(t) &= j_1(N(0), X_1(0), \dots, X_m(0), t), \\ &\dots \\ X_m(t) &= j_m(N(0), X_1(0), \dots, X_m(0), t), \end{aligned} \quad (D.2)$$

for some functions h, j_1, \dots, j_m . Although the latter are usually not known explicitly, it is theoretically possible to write a differential equation for $N(t)$ by replacing $X_1(t), \dots, X_m(t)$ in the first equation of the differential system:

$$\begin{aligned} \frac{dN(t)}{dt} &= f \left(N(t), j_1(N(0), X_1(0), \dots, X_m(0), t), \right. \\ &\left. \dots, j_m(N(0), X_1(0), \dots, X_m(0), t) \right). \end{aligned} \quad (D.3)$$

This equation shows that $\frac{dN(t)}{dt}$ is a function of $N(t)$, of the initial condition of the participating factors, and of t . Again, the appearance of $X_1(0), \dots, X_m(0)$ is not surprising, but it is striking to note the multiple presence of $N(0)$. The reduced equation is thus also dependent on the initial condition of the population of interest. This feature

discovered for simple biological systems appears to be very general and the same reasoning applies to any system of coupled differential equations, biological or not. Note that, for simplicity, we consider here reductions to one-dimensional equations. Clearly, any reduction to lower dimensions of a system of coupled differential equations entails the same difficulties.

Appendix E. Model reduction and uniqueness of solutions

The classical theory of ordinary differential equations deals with the form $\frac{dx(t)}{dt} = f(x(t), t)$, but the reduction of a system of two coupled equation yields the form $\frac{dx(t)}{dt} = f(x(0), x(t), t)$. For fixed initial condition $x(0)$, if the system would satisfy the usual properties of the classical form, then all properties would remain valid for the new form, in particular the existence and unicity of a solutions defined over a right-hand maximal time interval. We will focus on the special case of autonomous equations of the form $\frac{dx(t)}{dt} = f(x(0), x(t))$ and will present an equation that does not satisfy the unicity of solutions:

If $\frac{dx(t)}{dt} = (1 - x(0))x(t)$, then $x(t) = x(0)e^{(1-x(0))t}$ and thus for $x_1(0) = \frac{1}{2}$ and $x_2(0) = \frac{3}{2}$, the two solutions $x_1(t) = \frac{1}{2}e^{\frac{t}{2}}$ and $x_2(t) = \frac{3}{2}e^{-\frac{t}{2}}$ will cross each other for $t = \ln(3)$.

This example shows that the unicity of solutions can get lost in models of the form $\frac{dx(t)}{dt} = f(x(0), x(t))$, and consequently also in the more complex non-autonomous version.

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