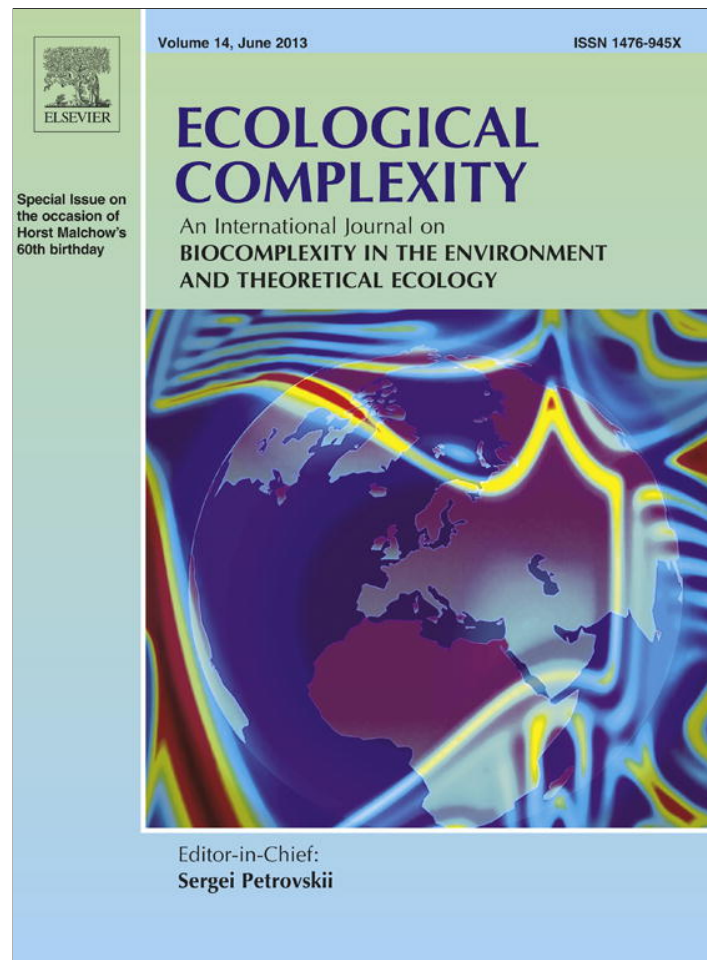


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Original research article

## Reduction of slow-fast asymptotically autonomous systems with applications to gradostat models

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## ABSTRACT

Two distinguishing features characterize the population dynamic models considered in the present work. On the one hand, we consider several interacting organization levels associated to different time scales. On the other hand, the environment tends to be constant in the long term. The mathematical representation of these properties leads to *slow-fast asymptotically autonomous* systems. These characteristics add some realism in the models. However, the analytical study of this class of systems is generally hard to perform.

Here we present a reduction technique that can be included among the so-called approximate aggregation methods. The existence of different time scales, together with the long term features, are used to build up a simpler system, which can be described by means of a lower number of state variables. The asymptotic behavior of the simplified model helps to study the original one.

The reduction procedure is formulated in a general way. Following, two illustrations of asymptotically autonomous models with two time scales, in a gradostat, are given: a consumer–resource model and a competition model. Finally, a wider range of applications is suggested.

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### 1. Introduction

An accurate description of systems in Nature needs combining different processes which are often related to specific scales. Hierarchy theory provides the conceptual framework of how processes and components of an ecological system interrelate and how they can be ordered (Lischke et al., 2007; Schneider, 2001) in different hierarchical levels. Simplifying the mathematical models representing these natural systems has to do with translating the effect of processes acting at a specific scale into an upper scale, what it is called *up-scaling*.

From a mathematical point of view, a model involving several interacting organization levels can be described through a system including several time scales. Indeed, each organization level consists of some interacting entities with their own dynamics. Those entities belonging to a given level with strong (or fast) interactions can be grouped giving rise to the entities at the next

level. For instance, a population can be seen as several sets of individuals, each set being characterized by a similar trait. This description, based on a structured population, can be useful to understand the role of the structure on the population dynamics. When considering a community, if possible, the different sub-populations are merged: the population as a whole is considered for the study at the community level.

Mathematically, the process of up-scaling consists in deriving global variables and their dynamics from those in the lower level. Roughly, this is done by considering the events occurring at the fastest scale as being instantaneous with respect to the slower ones. This consideration entails a reduction of the number of state variables and parameters needed to describe the dynamics of the system at the upper level. The so-called *aggregation methods* are an example of this general framework, see Auger et al. (2008, 2012) for recent reviews. These methods study the relationship between general classes of two time scale systems and their corresponding *aggregated* or reduced ones. In this way, they supply a rigorous support to simplifications that some models implicitly incorporate without any further justification. With these methods we can develop realistic models in a more detailed form, while keeping them mathematically tractable aided by an appropriate reduction of the dimension.

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Aggregation techniques for autonomous ordinary differential equations are well established. The approach is based upon the Fenichel theorems on persistence of invariant manifolds, Fenichel (1971), and on the geometric singular perturbation theory, Verhulst (2005, 2007). The general form of the system with two time scales in  $\mathbb{R}^m$  reads as follows:

$$\frac{dn}{d\tau} = f(n) + \varepsilon s(n), \quad (1)$$

where functions  $f$  and  $s$  describe, respectively, the fast and slow processes. The parameter  $\varepsilon$  is a small positive constant representing the ratio between time scales. We note  $\tau$  and  $t = \varepsilon\tau$ , respectively, the time variable in the fast and the slow time units. We assume that there exist some constants of motion for the fast part of the system, obtained with  $\varepsilon = 0$ . These constants of motion are called *global variables*. Then, a change of coordinates is performed in order to use them explicitly in the model. Since they are constant of motion for the fast part, it follows that they exhibit a slow dynamics. The remaining variables are called fast variables, which are assumed to reach an attractor (a stable equilibrium for instance). Note that this attractor may depend on the global variables. A reduced system, called aggregated system, for these global variables makes easier the study of the asymptotic behavior of system (1).

Autonomous systems, like (1), reflect the assumption of constant environment. A lot of ecological questions of interest involve variable environments and hence nonautonomous, or time dependent, systems. The general form of nonautonomous system with two time scales fits in the framework of singular perturbations by Hoppensteadt (1966, 1993, 2010). The drawback in applying these results lies in checking the assumptions, which may be a very technical and difficult task. A useful approach in this context, consists in finding particular forms of systems for which Hoppensteadt assumptions are easily proved to be met. When this goal is reached, a practical approximate aggregation technique is available. In Marva et al. (2012c) this program is carried out for systems with two time scales and periodic terms which period is of the order of the slow time scale. They could be written in the following form

$$\frac{dn}{d\tau} = f(\varepsilon\tau, n) + \varepsilon s(\varepsilon\tau, n),$$

where  $f$  and  $s$  are taken to be periodic functions of  $t = \varepsilon\tau$ . The reduction techniques presented in Marva et al. (2012c) are further applied to epidemic models in Marva et al. (2012a,b).

The goal of this work consist in presenting the aforementioned reduction procedure for a class of nonautonomous systems with two time scales, of the form:

$$\frac{dn}{d\tau} = f(\tau, n) + \varepsilon s(\tau, n),$$

where  $f$  and  $s$  are asymptotically autonomous (in the sequel, A.A.) functions. Roughly, an A.A. system could be described as a time dependent system such that the explicitly time varying terms tend to be constant (Thieme and Castillo-Chavez, 1995; Li and Wang, 2007). In other words, the explicit time dependence disappears in the long term. To illustrate what is an A.A. system in a simple context, let us consider a model of a population in a pond. We assume that water enter and leave the pond at the same rate so that its volume remains constant. The incoming water has a constant concentration of a certain substance that affects the species inhabiting the pond. Then, their environment inside the pond is variable and it is possible to describe their dynamics with a nonautonomous system. However, the amount of substance in the

pond tends to stabilize attaining the same concentration as in the incoming water. Consequently, the species vital rates depending on the substance concentration are eventually constant, i.e., the system is A.A.

A model with two time scales for two competing species inhabiting an A.A. environment, similar to the one just described above, is presented in Section 2.2. Subsequently, it is analyzed in Section 3.2 with the help of the reduction technique developed in Section 3.

The main results on A.A. systems are due to Markus (1956) and Thieme et al. (1995). Under certain conditions the asymptotic behavior of an A.A. system can be obtained from an associated autonomous system called limit system (the precise definitions can be found in Appendix A). The use of this limit system together with the results in Hoppensteadt (1966, 1993, 2010) provide the reduction procedure that we present and apply in this work.

Section 2 presents two models with two time scales. The one in Section 2.1 is autonomous. Solving it partially, for one of the variables, yields a new system with one variable less, but at the cost of becoming A.A. The model in Section 2.2 has already been mentioned. Section 3 is devoted to the presentation, step by step, of the reduction technique. This is followed by its application to the analysis of the models introduced in Section 2. All technical details and general results are collected in Appendix A. In Section 4, we discuss our results and suggest further applications, as for instance, how to deal with two time scale models coupling A.A. and periodic terms.

## 2. Two time scale asymptotically autonomous models

In this section we introduce two population models in a gradostat. Both include two time scales and can be represented by A.A. systems.

### 2.1. A consumer–resource model in a gradostat

The model presented here has not been analyzed elsewhere and it is related with the work in Loreau (1998, 2010) (in particular, pages 44–45 of the latter). There, it is addressed an ecosystem model consisting of  $N$  plants having limited access to an inorganic nutrient in individual depletion zones.

Here we consider a gradostat consisting of chemostats 1 and 2 connected as shown in Fig. 1. Both vessels are shared by primary producers and producers' nutrient, and vessel 2 also hosts consumers of primary producers. Variables  $S_i$  and  $P_i$  are the concentrations of nutrient and primary producers in vessel  $i = 1, 2$ , and variable  $Q$  is the concentration of consumers in vessel 2. Constant  $D$  denotes the dilution rate (1/time) that represents the inflow to vessel 1, the flow from vessel 1 to vessel 2, and the outflow from vessel 2, so that the medium in each chemostat remains constant. The concentration of the input nutrient is  $S_0$  (mass/volume) so that  $I = S_0D$  is the nutrient inflow (mass/time).

We assume, in the general case, that producers consumption rate is proportional to the availability of nutrient and so it has a general form  $v(S_i)P_i$ . In absence of consumers, the equations describing nutrient and producers concentration dynamics in each chemostat are

$$\begin{cases} \frac{dS_1}{d\tau} = I - DS_1 - v(S_1)P_1, \\ \frac{dS_2}{d\tau} = D(S_1 - S_2) - v(S_2)P_2, \\ \frac{dP_1}{d\tau} = \alpha_1 v(S_1)P_1 - DP_1, \\ \frac{dP_2}{d\tau} = DP_1 + \alpha_2 v(S_2)P_2 - DP_2, \end{cases} \quad (2)$$

where  $\alpha_i$ , for  $i = 1, 2$ , are positive constants denoting conversion efficiency factors.

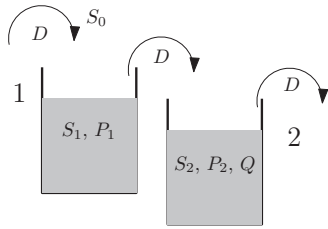


Fig. 1. Scheme of the gradostat.

When incorporating consumers into system (2), we assume that their vital processes are slow when compared to those of nutrients and primary producers. The consumers consumption rate of primary producers is given by the nonnegative bounded function  $\Upsilon(P_2, Q)$  that vanishes for  $P_2 = 0$  or  $Q = 0$ . Consumers concentration is supposed to follow a logistic growth law with constant growth rate  $\lambda$  and carrying capacity  $K(P_2)$ . Function  $K$  is nonnegative and bounded and verifies that  $\lim_{P_2 \rightarrow 0} K(P_2) = 0$ . Consumers do not move from chemostat 2. At this point we make no further assumptions on  $\Upsilon(P_2, Q)$  and  $K(P_2)$ .

In order to get an analytically tractable model we choose the following form for nutrient consumption rate  $v(S_i) = \xi S_i$ , where  $\xi$  is a positive constant. For the sake of simplicity we also consider  $\alpha_1 = \alpha_2 \equiv \alpha$ , what means that environmental conditions are identical in both chemostats.

The model including consumers that takes into account all the stated assumptions has the form:

$$\begin{cases} \frac{dS_1}{d\tau} = I - DS_1 - \xi S_1 P_1, \\ \frac{dS_2}{d\tau} = D(S_1 - S_2) - \xi S_2 P_2, \\ \frac{dP_1}{d\tau} = \alpha \xi S_1 P_1 - DP_1, \\ \frac{dP_2}{d\tau} = DP_1 + \alpha \xi S_2 P_2 - DP_2 - \varepsilon \Upsilon(P_2, Q), \\ \frac{dQ}{d\tau} = \varepsilon \lambda Q \left(1 - \frac{Q}{K(P_2)}\right), \end{cases} \quad (3)$$

where  $\varepsilon$  is the small positive constant representing the ratio between time scales.

System (3) is autonomous with two time scales. An appropriate change of variables allows solving for one of the new variables obtaining a less dimensional system, which is nonautonomous though A.A.

We first define the new variables  $\hat{S}_i = \alpha S_i$ , for  $i = 1, 2$ , and the new constant  $\hat{I} = \alpha I$  and we write again system (3) for them, though keeping notation without hat, obtaining

$$\begin{cases} \frac{dS_1}{d\tau} = I - DS_1 - \xi S_1 P_1, \\ \frac{dS_2}{d\tau} = D(S_1 - S_2) - \xi S_2 P_2, \\ \frac{dP_1}{d\tau} = \xi S_1 P_1 - DP_1, \\ \frac{dP_2}{d\tau} = DP_1 + \xi S_2 P_2 - DP_2 - \varepsilon \Upsilon(P_2, Q), \\ \frac{dQ}{d\tau} = \varepsilon \lambda Q \left(1 - \frac{Q}{K(P_2)}\right). \end{cases} \quad (4)$$

If we consider now the total concentration of nutrient and primary producers in chemostat 1,  $B_1 = S_1 + P_1$ , we see that it satisfies the equation

$$\frac{dB_1}{d\tau} = I - DB_1,$$

which solution, for a given initial condition  $B_1(0)$ , is

$$B_1(\tau) = S_0 + e^{-D\tau}(B_1(0) - S_0).$$

We can interpret the new variable  $B_1$  as the total concentration of potential resource in chemostat 1 available for individuals in chemostat 2. We point out that the contribution of  $S_1$  and  $P_1$  to  $S_0$ , the asymptotic value of  $B_1(\tau)$ , can vary. We can eliminate variable  $S_1$  in system (4) by using the substitution  $S_1 = B_1 - P_1$  what yields

$$\begin{cases} \frac{dS_2}{d\tau} = D(B_1(\tau) - P_1 - S_2) - \xi S_2 P_2, \\ \frac{dP_1}{d\tau} = \xi(B_1(\tau) - P_1)P_1 - DP_1, \\ \frac{dP_2}{d\tau} = DP_1 + \xi S_2 P_2 - DP_2 - \varepsilon \Upsilon(P_2, Q), \\ \frac{dQ}{d\tau} = \varepsilon \lambda Q \left(1 - \frac{Q}{K(P_2)}\right), \end{cases} \quad (5)$$

which is a A.A. system since  $\lim_{\tau \rightarrow \infty} B_1(\tau) = S_0$ . We can see  $B_1$  as a time varying environmental constrain that tends to a constant value in the long term.

### 2.2. A competition two time scale model in a gradostat

The model proposed in this section is inspired in Li and Wang (2007), where a problem on environmental toxicology was addressed. Namely, the authors considered an A.A. system describing the dynamics of a mutualistic community inhabiting a polluted environment such that the amount of pollutant is changing but tends to a constant level in the long term.

We consider here a gradostat which schematic diagram is presented in Fig. 2. It consists of two identical chemostats, connected so that a flow between them occurs, and such that each chemostat has a separate inflow and outflow to the outside environment. In the gradostat there are two competing species affected by a pollutant input from an external source. We assume that the pollutant moves all across the gradostat while both species keep in the gradostat and can only move from one vessel to the other. A final assumption is that both pollutant and species transfers are fast compared to species demography.

For  $i, j = 1, 2$ , let  $n_{ij}(\tau)$  denote the size of the species  $j$  and  $S_i(\tau)$  the concentration of pollutant in chemostat  $i$  at time  $\tau$ . Positive parameters  $m_i$ ,  $m_i^{in}$  and  $m_i^{out}$ ,  $i = 1, 2$ , represent the different medium transference flows and their units are volume/time. These rates keep constant the medium volumes, that we consider equals to 1, in both vessels. The species transference rates are assumed to be  $\delta m_1$  for displacements from chemostat 1 to chemostat 2 and  $\delta m_2$  in the other sense, where  $\delta$  is a positive parameter. Constant  $e_i$  is the concentration of the pollutant entering chemostat  $i$ ,  $i = 1, 2$ , mass/volume.

Competition in each chemostat is described by a Lotka–Volterra model where  $\lambda_j$ , species  $j$  growth rate,  $K_j$ , species  $j$  carrying capacity, and  $a_j$ , competition coefficient on species  $j$ ,  $j = 1, 2$ , depend on  $S_i(\tau)$ , the concentration of pollutant in the chemostat  $i$ ,

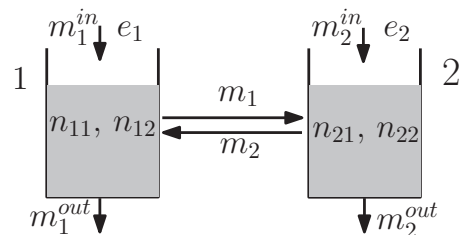


Fig. 2. Scheme of the gradostat.

$i = 1, 2$ . Finally, the system takes the form

$$\begin{cases} \frac{dS_1}{d\tau} = -(m_1 + m_1^{out})S_1 + m_2S_2 + m_1^{in}e_1, \\ \frac{dS_2}{d\tau} = m_1S_1 - (m_2 + m_2^{out})S_2 + m_2^{in}e_2, \\ \frac{dn_{11}}{d\tau} = -\delta m_1n_{11} + \delta m_2n_{21} + \varepsilon\lambda_1(S_1)n_{11} \left(1 - \frac{n_{11} + a_1(S_1)n_{12}}{K_1(S_1)}\right), \\ \frac{dn_{21}}{d\tau} = \delta m_1n_{11} - \delta m_2n_{21} + \varepsilon\lambda_1(S_2)n_{21} \left(1 - \frac{n_{21} + a_1(S_2)n_{22}}{K_2(S_2)}\right), \\ \frac{dn_{12}}{d\tau} = -\delta m_1n_{12} + \delta m_2n_{22} + \varepsilon\lambda_2(S_1)n_{12} \left(1 - \frac{n_{12} + a_2(S_1)n_{11}}{K_1(S_1)}\right), \\ \frac{dn_{22}}{d\tau} = \delta m_1n_{22} - \delta m_2n_{12} + \varepsilon\lambda_2(S_2)n_{22} \left(1 - \frac{n_{22} + a_2(S_2)n_{21}}{K_2(S_2)}\right). \end{cases} \quad (6)$$

where, as usual,  $\varepsilon$  is the small positive parameter representing the ratio between time scales. Pollutant equations form themselves a linear, uncoupled system which can be straightforwardly solved. Substituting the explicit solution  $(S_1(\tau), S_2(\tau))$  into the equations of species population sizes,  $n_{ij}$ , we get the following four dimensional nonautonomous system with two time scales.

$$\begin{cases} \frac{dn_{11}}{d\tau} = -\delta m_1n_{11} + \delta m_2n_{21} + \varepsilon\lambda_1(S_1(\tau))n_{11} \left(1 - \frac{n_{11} + a_1(S_1(\tau))n_{12}}{K_1(S_1(\tau))}\right), \\ \frac{dn_{21}}{d\tau} = \delta m_1n_{11} - \delta m_2n_{21} + \varepsilon\lambda_1(S_2(\tau))n_{21} \left(1 - \frac{n_{21} + a_1(S_2(\tau))n_{22}}{K_2(S_2(\tau))}\right), \\ \frac{dn_{12}}{d\tau} = -\delta m_1n_{12} + \delta m_2n_{22} + \varepsilon\lambda_2(S_1(\tau))n_{12} \left(1 - \frac{n_{12} + a_2(S_1(\tau))n_{11}}{K_1(S_1(\tau))}\right), \\ \frac{dn_{22}}{d\tau} = \delta m_1n_{22} - \delta m_2n_{12} + \varepsilon\lambda_2(S_2(\tau))n_{22} \left(1 - \frac{n_{22} + a_2(S_2(\tau))n_{21}}{K_2(S_2(\tau))}\right), \end{cases} \quad (7)$$

which is A.A. since  $\lim_{t \rightarrow \infty} S_i(t) = \bar{S}_i$ ,  $i = 1, 2$ , where equilibrium  $(\bar{S}_1, \bar{S}_2)$  is the solution of system

$$\begin{cases} 0 = -(m_1 + m_1^{out})S_1 + m_2S_2 + m_1^{in}e_1, \\ 0 = m_1S_1 - (m_2 + m_2^{out})S_2 + m_2^{in}e_2. \end{cases}$$

### 3. Approximate aggregation of two time scales asymptotically autonomous systems. Analysis of systems (4) and (6)

The analysis of systems (4) and (6) relies on a reduction technique whose mathematical justification is addressed in Appendix A. For the convenience of the reader we present here a step-by-step description (how-to) of this technique. System (6) is of the general two time scale systems form

$$\frac{dn}{d\tau} = f(\tau, n) + \varepsilon s(\tau, n), \quad (8)$$

described in the introduction while system (5) is already in the so-called *slow-fast* form

$$\begin{cases} \frac{dx}{d\tau} = F(\tau, x, y) + \varepsilon H(\tau, x, y), \\ \frac{dy}{d\tau} = \varepsilon S(\tau, x, y). \end{cases} \quad (9)$$

where variables  $x$  and  $y$  are known as *fast* and *slow* variables, respectively. Though there is no general rule to transform the two time scale system (8) into its slow-fast form (9), in concrete applications it is possible to derive such a change of variables

$n \mapsto (x, y)$  having in mind that slow variables are invariant for the fast dynamics. In Section 3.2 we see for system (6) that the total population size of each species is invariant for the fast process which is given by the displacements between chemostats.

Let us describe the reduction procedure.

1 *Get the limit system.* Functions  $F, H, S$  are A.A. and we can calculate  $\bar{J}(x, y) = \lim_{\tau \rightarrow \infty} J(\tau, x, y)$ , for  $J \in \{F, H, S\}$ . The limit functions  $\bar{J}$  describe (roughly) the value of the derivatives of  $x, y$  for very large time values, which tend toward a constant value. With its help we set up the *limit* (autonomous) system

$$\begin{cases} \frac{dx}{d\tau} = \bar{F}(x, y) + \varepsilon \bar{H}(x, y), \\ \frac{dy}{d\tau} = \varepsilon \bar{S}(x, y). \end{cases} \quad (10)$$

2 *Find the fast equilibria.* We consider  $y$  as a parameter and look for the asymptotically stable equilibria of equation

$$\frac{dx}{d\tau} = \bar{F}(x, y).$$

First we solve for  $x^*(y)$  equation

$$0 = \bar{F}(x^*(y), y),$$

and then we must prove the asymptotic stability of  $x^*(y)$ . In particular, we can do it by linearization, that is, we check that all the eigenvalues of the Jacobian matrix

$$J_x \bar{F}(x^*(y), y)$$

have negative real parts for every  $y$  in the corresponding domain.

These equilibria are known as *fast equilibria*.

3 *Build up the aggregated system.* Finally, we substitute  $x$  by  $x^*(y)$  in the second equation of system (10) and change  $\tau$  into  $t = \varepsilon\tau$  to obtain the *aggregated system* for the slow (global) variables

$$\frac{dy}{dt} = \bar{S}(x^*(y), y). \quad (11)$$

Under certain hypotheses (see Appendix A) the asymptotic behavior of system (9) (or the equivalent system (8)) can be described by means of the fast equilibria  $x^*(y)$  and asymptotically stable solutions of system (11).

It is interesting to point out that there are as many aggregated systems as different manifolds  $x^*(y)$  of fast equilibria (see, for instance, Auger et al. (2009)).

In the following, we apply this technique to the study of the models presented in Section 2.

#### 3.1. Analysis of system (4)

We study system (4) by means of the equivalent A.A. system (5). In order to relate system (5) and the A.A. prototype (9) we can take as fast variables  $x = (S_2, P_1, P_2)$  and as slow variable  $y = Q$  and thus

$$F(\tau, x, y) = \begin{pmatrix} D(B_1(\tau) - P_1 - S_2) - \xi S_2 P_2 \\ \xi(B_1(\tau) - P_1)P_1 - DP_1 \\ DP_1 + \xi S_2 P_2 - DP_2 \end{pmatrix}^T$$

$$H(\tau, x, y) = (0, 0, \mathcal{Y}(P_2, Q)) \quad \text{and} \quad S(\tau, x, y) = \lambda Q \left(1 - \frac{Q}{K(P_2)}\right),$$



where  $T$  denotes transposition. We now follow the step-by-step reduction procedure:

1 The corresponding *limit system* is obtained replacing  $B_1(\tau)$  by  $\lim_{\tau \rightarrow \infty} B_1(\tau) = S_0$ , obtaining

$$\begin{cases} \frac{dS_2}{d\tau} = D(S_0 - P_1 - S_2) - \xi S_2 P_2, \\ \frac{dP_1}{d\tau} = \xi(S_0 - P_1)P_1 - DP_1, \\ \frac{dP_2}{d\tau} = DP_1 + \xi S_2 P_2 - DP_2 - \varepsilon \Upsilon(P_2, Q), \\ \frac{dQ}{d\tau} = \varepsilon \lambda Q \left(1 - \frac{Q}{K(P_2)}\right). \end{cases}$$

Thus,  $\bar{F}(x, y)$ , which does not depend on  $y$ , is

$$\bar{F}(x) = \begin{pmatrix} D(S_0 - P_1 - S_2) - \xi S_2 P_2 \\ \xi(S_0 - P_1)P_1 - DP_1 \\ DP_1 + \xi S_2 P_2 - DP_2 \end{pmatrix}^T,$$

$$\bar{H}(x, y) = (0, 0, \Upsilon(P_2, Q)) \quad \text{and} \quad \bar{s}(x, y) = \lambda Q \left(1 - \frac{Q}{K(P_2)}\right),$$

2 To find the *fast equilibria* we look for the nonnegative asymptotic stable equilibria of system

$$\frac{dx}{d\tau} = \bar{F}(x). \tag{12}$$

First we solve  $0 = \bar{F}(x)$ , obtaining

$$E_1^* = (S_0, 0, 0), \quad E_2^* = \left(\frac{D}{\xi}, 0, S_0 - \frac{D}{\xi}\right),$$

$$E_3^* = \left(\hat{S}_{2-}^*, S_0 - \frac{D}{\xi}, S_0 - \hat{S}_{2-}^*\right), \quad E_4^* = \left(\hat{S}_{2+}^*, S_0 - \frac{D}{\xi}, S_0 - \hat{S}_{2+}^*\right),$$

where

$$\hat{S}_{2-}^* = \frac{\xi S_0 + D - \sqrt{(\xi S_0 + D)^2 - 4D^2}}{2\xi}$$

and

$$\hat{S}_{2+}^* = \frac{\xi S_0 + D + \sqrt{(\xi S_0 + D)^2 - 4D^2}}{2\xi}.$$

We discard solution  $E_1^*$  because it does not make sense in system (4) noticing that  $P_2 = 0$  yields  $K(P_2) = 0$ . On the other hand, if  $\xi S_0 - D < 0$  we see that  $E_2^*, E_3^*$  and  $E_4^*$  have some negative components and thus we can also discard those cases. Finally, if  $\xi S_0 - D > 0$  by linearization we obtain that the only nonnegative equilibrium which is asymptotically stable is  $E_3^*$ .

3 In the last step, using  $x^*(y) = E_3^*$ , for any  $y = Q$ , we get the corresponding *aggregated system*, that simply consists of equation

$$\frac{dQ}{dt} = \lambda Q \left(1 - \frac{Q}{K(S_0 - \hat{S}_{2-}^*)}\right) \tag{13}$$

which analysis is straightforward: any solution with positive initial condition is in the domain of attraction of equilibrium  $Q^* = K(S_0 - \hat{S}_{2-}^*)$ .

**Theorem 2** on the asymptotic behavior of system (4), for the case  $\xi S_0 - D > 0$ , is a direct application of **Theorem 6** in **Appendix A**. The result is expressed in terms of equilibrium  $E_3^*$  of system (12) (see step 2) and equilibrium  $Q^*$  of system (13) (see step 3) together with their domains of attraction. For  $Q^*$  we already said that it attracts every

solution with  $Q(0) > 0$  and we see in the next lemma, before stating **Theorem 2**, a similar result for  $E_3^*$ .

**Lemma 1.** *Let  $x(t) := (S_2(t), P_1(t), P_2(t))$  be the solution of system (12) with initial conditions  $S_{20} \geq 0, P_{10} > 0$  y  $P_{20} \geq 0$ . Then*

$$\lim_{t \rightarrow \infty} x(t) = E_3^*$$

**Proof.** The equation for  $P_1$  in system (12),  $P_1' = \xi(S_0 - P_1)P_1 - DP_1$ , is scalar autonomous and it is straightforward to prove that for any initial condition  $P_{10} > 0$  the corresponding solution  $P_1(t)$  verifies  $\lim_{t \rightarrow \infty} P_1(t) = S_0 - D/\xi$ .

Adding up the equations for  $S_2$  and  $P_2$  we obtain that

$$(S_2 + P_2)' = DS_0 - D(S_2 + P_2).$$

The explicit solution of this linear equation leads to  $\lim_{t \rightarrow \infty} (S_2(t) + P_2(t)) = S_0$  for any initial conditions, in particular if  $S_{20}, P_{20} \geq 0$ .

We have, therefore, that solutions of system (12) with the prescribed initial conditions are attracted to the closed invariant set

$$\Gamma = \left\{ (S_2, P_1, P_2) \in \mathbb{R}_+^3 : P_1 = S_0 - \frac{D}{\xi}, S_2 + P_2 = S_0 \right\}.$$

On  $\Gamma$  the dynamics of system (12) can be expressed through the following equation for  $S_2$

$$\begin{aligned} S_2' &= D \left( S_0 - \left( S_0 - \frac{D}{\xi} \right) - S_2 \right) - \xi S_2 (S_0 - S_2) \\ &= \xi S_2^2 - (\xi S_0 + D) S_2 + \frac{D^2}{\xi} \end{aligned}$$

A direct analysis of equilibria stability of this scalar autonomous equation yields that for any initial condition  $S_{20} \in [0, S_0]$  the corresponding solution tends to  $\hat{S}_{2+}^*$ .

We can conclude that the  $\omega$ -limit set on any solution of system (12) with initial conditions  $S_{20} \geq 0, P_{10} > 0$  y  $P_{20} \geq 0$  consist of the asymptotically stable equilibria  $E_3^*$ , what proves the lemma.  $\square$

**Theorem 2.** *Let  $X_\varepsilon(t) := (S_1^\varepsilon(t), S_2^\varepsilon(t), P_1^\varepsilon(t), P_2^\varepsilon(t), Q^\varepsilon(t))$  be the solution of system (4) with  $\varepsilon > 0$  and initial conditions  $(S_{10}, S_{20}, P_{10}, P_{20}, Q_0) \in \mathbb{R}_+^5, P_{10} > 0$  and  $Q_0 > 0$ . If  $\xi S_0 - D > 0$  then, for any  $\delta > 0$ , there exist  $\varepsilon_\delta > 0$  and  $t_\delta > 0$  such that*

$$\left| X_\varepsilon(t) - \left( \frac{D}{\xi}, \hat{S}_{2-}^*, S_0 - \frac{D}{\xi}, S_0 - \hat{S}_{2-}^*, K(S_0 - \hat{S}_{2-}^*) \right) \right| < \delta,$$

for every  $\varepsilon \leq \varepsilon_\delta$  and  $t \geq t_\delta$ .

To complete the study of system (4) we have the following result stating that if  $\xi S_0 - D < 0$  then primary producers,  $P_1$  and  $P_2$ , and consumers,  $Q(t)$ , tend to disappear from the gradostat.

**Theorem 3.** *Let  $X_\varepsilon(t) := (S_1^\varepsilon(t), S_2^\varepsilon(t), P_1^\varepsilon(t), P_2^\varepsilon(t), Q^\varepsilon(t))$  be the solution of system (4) with initial conditions  $(S_{10}, S_{20}, P_{10}, P_{20}, Q_0) \in \mathbb{R}_+^5$ . If  $\xi S_0 - D < 0$  then*

$$\lim_{t \rightarrow \infty} X_\varepsilon(t) = (S_0, S_0, 0, 0, 0).$$

**Proof.** We consider all along the proof that  $(S_1, S_2, P_1, P_2, Q) \in \mathbb{R}_+^5$ , which is a positively invariant set for system (4).

Let  $\delta > 0$  be such that

$$\xi S_0 - D < -\delta \tag{14}$$

1 We first prove that  $\lim_{t \rightarrow \infty} P_1(\tau) = 0$  and  $\lim_{t \rightarrow \infty} S_1(\tau) = S_0$ .

We already showed, after the presentation of system (4), that

$$\lim_{\tau \rightarrow \infty} (S_1(\tau) + P_1(\tau)) = S_0 \tag{15}$$

The equation for  $P_1$  is

$$\frac{dP_1}{d\tau} = \xi S_1 P_1 - DP_1 = (\xi(S_1 + P_1) - D)P_1 - \xi P_1^2$$

From (14) and (15) we can find  $\tau_1 > 0$  such that for every  $\tau \geq \tau_1$  it is verified that  $\xi(S_1 + P_1) - D \leq -\delta$  and thus we have

$$\frac{dP_1}{d\tau} \leq -\delta P_1$$

what implies that  $\lim_{t \rightarrow \infty} P_1(\tau) = 0$  and consequently  $\lim_{t \rightarrow \infty} S_1(\tau) = S_0$ .

2 Next we prove that for any  $\epsilon > 0$  there exists  $\tau_\epsilon$  such that, for  $\tau \geq \tau_\epsilon$ ,  $S_2(\tau) \leq S_0 + \epsilon$ :

$$\frac{dS_2}{d\tau} = D(S_1 - S_2) - \xi S_2 P_2 \leq D(S_1 - S_2)$$

hence

$$\frac{dS_2}{d\tau} + DS_2 \leq DS_1; \quad \frac{d}{d\tau}(e^{D\tau} S_2) \leq De^{D\tau} S_1$$

and integrating on  $[0, \tau]$  yields

$$S_2(\tau) \leq e^{-D\tau} S_{20} + e^{-D\tau} \int_0^\tau De^{Ds} S_1(s) ds.$$

Using that  $\lim_{t \rightarrow \infty} S_1(\tau) = S_0$  it is straightforward that we can find  $\tau_\epsilon$  verifying the required conditions.

3 The inequality in (ii) allows proving that  $\lim_{t \rightarrow \infty} P_2(\tau) = 0$ .

Let  $\epsilon = 1/2\delta/\xi$  and call  $\tau_\epsilon = \tau_2$

$$\begin{aligned} \frac{dP_2}{d\tau} &= DP_1 + \xi S_2 P_2 - DP_2 - \epsilon \Upsilon(P_2, Q) \leq (\xi S_2 - D)P_2 + DP_1 \\ &\leq -\frac{\delta}{2} P_2 + DP_1 \end{aligned}$$

that, using the integration procedure shown in (ii) on the interval  $[\tau_2, \tau]$ , yields

$$P_2(\tau) \leq e^{-\frac{\delta}{2}(\tau-\tau_2)} P_2(\tau_2) + e^{-\frac{\delta}{2}\tau} \int_{\tau_2}^\tau De^{\frac{\delta}{2}s} P_1(s) ds$$

which together with  $\lim_{t \rightarrow \infty} P_1(\tau) = 0$  gives  $\lim_{t \rightarrow \infty} P_2(\tau) = 0$ .

4 We can now prove that  $\lim_{t \rightarrow \infty} S_2(\tau) = S_0$ .

For that, having in mind (ii), it is enough to show that for any  $\epsilon > 0$  there exists  $\bar{\tau}_\epsilon$  such that, for  $\tau \geq \bar{\tau}_\epsilon$ ,  $S_2(\tau) \geq S_0 - \epsilon$ . This can be obtained from  $\lim_{t \rightarrow \infty} P_2(\tau) = 0$  which gives

$$\frac{dS_2}{d\tau} = D(S_1 - S_2) - \xi S_2 P_2 \leq D(S_1 - S_2) - \bar{\epsilon} S_2,$$

for any  $\bar{\epsilon} > 0$  and  $\tau$  big enough, by using a similar integration procedure to those used in (ii) and (iii) together with the fact that  $\lim_{t \rightarrow \infty} S_1(\tau) = S_0$ .

5 Finally we prove that  $\lim_{t \rightarrow \infty} Q(\tau) = 0$ .

The equation for  $Q$  by means of the appropriate unity change in the time variable can be written in the following form:

$$\frac{dQ}{dt} = Q \left( 1 - \frac{Q}{K(P_2)} \right)$$

As  $K$  is a bounded function and  $dQ/dt < 0$  if  $Q(t) > K(P_2(t))$  any solution  $Q(t)$  is bounded from above; let  $B_Q$  be an upper bound of the solution  $Q(t)$ . From  $\lim_{t \rightarrow \infty} P_2(t) = 0$  and  $\lim_{P_2 \rightarrow 0} K(P_2) = 0$  we have that for each  $\epsilon > 0$  there exists  $t_\epsilon > 0$  such that  $K(P_2(t)) < \epsilon$  for every  $t > t_\epsilon$ . Thus, for every  $t > t_\epsilon$  it holds that

$$\frac{dQ}{dt} \leq B_Q \left( 1 - \frac{Q}{\epsilon} \right)$$

and the usual integration procedure in this linear differential inequality yields that  $\lim_{t \rightarrow \infty} Q(\tau) = 0$ .  $\square$

Now, we illustrate the previous results with numerical simulations in Figs. 3 and 4. We display the results obtained calculating the solutions with the complete system (4) and with the aggregated system (along with the fast equilibria).

### 3.2. Analysis of system (6)

We study system (6) by means of the equivalent A.A. system (7), which is in the form (8).

To apply the reduction procedure to system (7) we first need to transform it into the slow-fast form (9). For that we must find the slow variables and here we have two natural candidates: each species total size, that we denote  $n_j := n_{1j} + n_{2j}$ ,  $j = 1, 2$ . These quantities keep invariant for the fast dynamic since  $d(n_{1j} + n_{2j})/d\tau = 0$  when  $\epsilon = 0$  in system (7), that is, total species sizes do not vary with individual movements between vessels.

The next change of variables

$$(n_{11}, n_{21}, n_{12}, n_{22}) \mapsto (n_{11}, n_{12}, n_1, n_2),$$

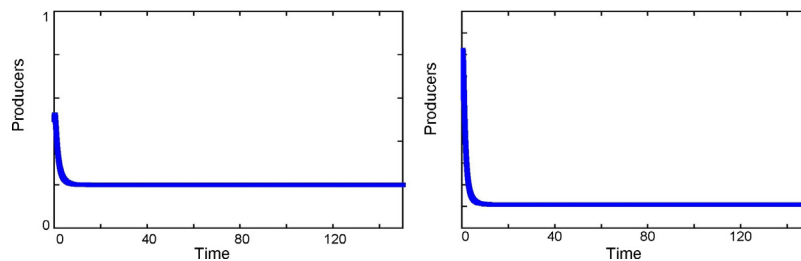
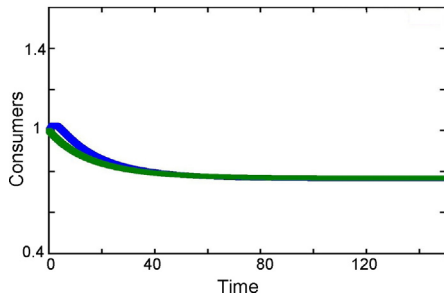


Fig. 3. Concentration of primary producers in chemostat 1 (left) and 2 (right) calculated with the complete system. The asymptotic values rapidly approach the equilibrium values given by the fast equilibria. We have considered  $\Upsilon(P_2, Q) = \eta P_2 Q$  and  $K(P_2) = KP_2$ . Parameter values:  $\epsilon = 0.01$ ,  $\eta = 0.8$ ,  $K = 1.5$ ,  $\lambda = 5$ ,  $D = 2$ ,  $\xi = 2.5$ ,  $I = 2$ .



**Fig. 4.** Comparison between the concentration of consumers calculated with the complete system (blue) and the aggregated system (green). We have considered  $Y(P_2, Q) = \eta P_2 Q$  and  $K(P_2) = KP_2$ . Parameter values:  $\varepsilon = 0.01$ ,  $\eta = 0.8$ ,  $K = 1.5$ ,  $\lambda = 5$ ,  $D = 2$ ,  $\xi = 2.5$ ,  $I = 2$ . Note that the limit value of  $Q(\tau)$  is not  $K$  but  $K \cdot P_2$ . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

leads to the following equivalent system in slow-fast form, where  $n_{11}$  and  $n_{12}$  are the fast variables and  $n_1$  and  $n_2$  the slow ones.

$$\begin{cases} \frac{dn_{11}}{d\tau} = -\delta m_1 n_{11} + \delta m_2 (n_1 - n_{11}) + \varepsilon \lambda_1 (S_1(\tau)) n_{11} \left(1 - \frac{n_{11} + a_1(S_1(\tau)) n_{12}}{K_1(S_1(\tau))}\right), \\ \frac{dn_{12}}{d\tau} = -\delta m_1 n_{12} + \delta m_2 (n_2 - n_{12}) + \varepsilon \lambda_1 (S_1(\tau)) n_{12} \left(1 - \frac{n_{12} + a_2(S_1(\tau)) n_{11}}{K_2(S_1(\tau))}\right), \\ \frac{dn_1}{d\tau} = \varepsilon \lambda_1 (S_1(\tau)) n_{11} \left(1 - \frac{n_{11} + a_1(S_1(\tau)) n_{12}}{K_1(S_1(\tau))}\right) + \varepsilon \lambda_1 (S_2(\tau)) (n_1 - n_{11}) \left(1 - \frac{(n_1 - n_{11}) + a_1(S_2(\tau)) (n_2 - n_{12})}{K_1(S_2(\tau))}\right), \\ \frac{dn_2}{d\tau} = \varepsilon \lambda_2 (S_1(\tau)) n_{12} \left(1 - \frac{n_{12} + a_2(S_1(\tau)) n_{11}}{K_2(S_1(\tau))}\right) + \varepsilon \lambda_2 (S_2(\tau)) (n_2 - n_{12}) \left(1 - \frac{(n_2 - n_{12}) + a_2(S_2(\tau)) (n_1 - n_{11})}{K_2(S_2(\tau))}\right), \end{cases} \quad (16)$$

We can now follow the step-by-step reduction procedure as we did in Section (3.1):

- 1 The *limit system* is got replacing  $S_i$  by its limit  $\bar{S}_i$ ,  $i = 1, 2$  in system (16).
- 2 The only *fast equilibrium*, for every constant value of the slow variables  $n_1$  and  $n_2$ , is the solution of system

$$\begin{cases} 0 = -\delta m_1 n_{11} + \delta m_2 (n_1 - n_{11}), \\ 0 = -\delta m_1 n_{12} + \delta m_2 (n_2 - n_{12}), \end{cases}$$

that is,

$$n_{1i}^* = \mu_1^* n_i, \quad i = 1, 2, \quad \text{where } \mu_1^* = \frac{m_2}{m_1 + m_2}$$

which describe the asymptotic distribution of individuals of species  $i$  in the first chemostat. It is straightforward to check that, for constant  $n_1$  and  $n_2$ ,  $(n_{11}^*, n_{12}^*)$  is a globally asymptotically stable equilibrium of system

$$\begin{aligned} \frac{dn_{11}}{d\tau} &= -\delta m_1 n_{11} + \delta m_2 (n_1 - n_{11}); \\ \frac{dn_{12}}{d\tau} &= -\delta m_1 n_{12} + \delta m_2 (n_2 - n_{12}) \end{aligned}$$

- 3 Finally, we replace in the slow variables equations the fast variables by the fast equilibria and change time variable to  $t = \varepsilon \tau$ , getting the *aggregated system* which, rearranging terms, reads as follows:

$$\begin{cases} \frac{dn_1}{dt} = \bar{\lambda}_1 n_1 \left(1 - \frac{n_1 - \alpha_{12} n_2}{\bar{K}_1}\right), \\ \frac{dn_2}{dt} = \bar{\lambda}_2 n_2 \left(1 - \frac{n_2 - \alpha_{21} n_1}{\bar{K}_2}\right), \end{cases} \quad (17)$$

where we call  $\mu_2^* = 1 - \mu_1^*$  and for  $i = 1, 2$

$$\bar{\lambda}_i = \mu_1^* \lambda_i(\bar{S}_1) + \mu_2^* \lambda_i(\bar{S}_2),$$

$$\frac{1}{\bar{K}_i} = \frac{1}{\bar{\lambda}_i} \left( \frac{(\mu_1^*)^2 \lambda_i(\bar{S}_1)}{K_i(\bar{S}_1)} + \frac{(\mu_2^*)^2 \lambda_i(\bar{S}_2)}{K_i(\bar{S}_2)} \right),$$

$$\beta_i = \frac{1}{\bar{\lambda}_i} \left( \frac{(\mu_1^*)^2 \lambda_i(\bar{S}_1) a_i(\bar{S}_1)}{K_i(\bar{S}_1)} + \frac{(\mu_2^*)^2 \lambda_i(\bar{S}_2) a_i(\bar{S}_2)}{K_i(\bar{S}_2)} \right),$$

$$\alpha_{12} = \beta_1 \bar{K}_1 \quad \text{and} \quad \alpha_{21} = \beta_2 \bar{K}_2.$$

The reduced system (17) is the classical Lotka–Volterra competition model and its analysis can be found, for instance, in Murray (1993). It is important to note that the parameters of the aggregated system depend on both displacement rates and the limit values of  $S_i(\tau)$ ,  $i = 1, 2$ . Thus, we have incorporated the effect of fast dynamics to the slow process, which entails the dimension reduction.

The following conclusions on the asymptotic behaviour of solutions of system (6) are a direct consequence of the known results of classical system (17) and Theorem 6 in Appendix A.

**Theorem 4.** Let  $X_\varepsilon(t) := (S_1^\varepsilon(t), S_2^\varepsilon(t), n_{11}^\varepsilon(t), n_{12}^\varepsilon(t), n_1^\varepsilon(t), n_2^\varepsilon(t))$  be any solution of system (6) with initial conditions in  $\mathbb{R}_+^6$ . Then,

- 1 If  $\alpha_{12} \bar{K}_2 < \bar{K}_1$  and  $\alpha_{21} \bar{K}_1 < \bar{K}_2$  there is coexistence, that is, for any  $\delta > 0$ , there exist  $\varepsilon_\delta > 0$  and  $t_\delta > 0$  such that, for every  $\varepsilon \leq \varepsilon_\delta$  and  $t \geq t_\delta$ ,

$$|X_\varepsilon(t) - \Lambda^*| < \delta,$$

where  $\Lambda^* = (\bar{S}_1, \bar{S}_2, \mu_1^* n_1^*, \mu_1^* n_2^*, \mu_1^* n_1^*, \mu_2^* n_2^*)$  and  $(n_1^*, n_2^*)$  is the positive equilibrium of system (17).

- 2 If  $\alpha_{12} \bar{K}_2 < \bar{K}_1$  and  $\alpha_{21} \bar{K}_1 > \bar{K}_2$  then species 1 excludes species 2, that is, for any  $\delta > 0$ , there exist  $\varepsilon_\delta > 0$  and  $t_\delta > 0$  such that, for every  $\varepsilon \leq \varepsilon_\delta$  and  $t \geq t_\delta$ ,

$$|X_\varepsilon(t) - \Lambda^*| < \delta,$$

where  $\Lambda^* = (\bar{S}_1, \bar{S}_2, \mu_1^* \bar{K}_1, \mu_2^* \bar{K}_1, 0, 0)$ . Reversing the first inequalities it is expressed analogously that species 2 excludes species 1.

- 3 If  $\alpha_{12} \bar{K}_2 > \bar{K}_1$  and  $\alpha_{21} \bar{K}_1 > \bar{K}_2$  then there is exclusion of one or the other species depending on the initial conditions, that is, for any  $\delta > 0$ , there exist  $\varepsilon_\delta > 0$  and  $t_\delta > 0$  such that, for every  $\varepsilon \leq \varepsilon_\delta$  and  $t \geq t_\delta$ ,

$$|X_\varepsilon(t) - \Lambda^*| < \delta,$$

where  $\Lambda^* = (\bar{S}_1, \bar{S}_2, \mu_1^* \bar{K}_1, \mu_2^* \bar{K}_1, 0, 0)$  (resp.  $\Lambda^* = (\bar{S}_1, \bar{S}_2, 0, 0, \mu_1^* \bar{K}_2, \mu_2^* \bar{K}_2)$ ), if  $(n_{11}(0) + n_{21}(0), n_{12}(0) + n_{22}(0))$  is in the domain of attraction of equilibrium  $(\bar{K}_1, 0)$  of system (17) (resp. in the domain of attraction of  $(0, \bar{K}_2)$ ).



#### 4. Discussion and perspectives

The present work proposes a reduction method for asymptotically autonomous systems with two time scales. These systems represent an important class of population models where two families of processes act at different time scales and the terms describing the environment variability tend to reach steady values. The general form of the systems considered here is

$$\frac{dn}{d\tau} = f(\tau, n) + \varepsilon s(\tau, n).$$

The processes represented by  $f(\tau, n)$  are much faster than those represented by  $s(\tau, n)$ . The ratio between the orders of magnitude of the fast and the slow process rates is marked by the presence of the multiplicative constant  $\varepsilon$ . A crucial assumption is that the system can be transformed, by means of an appropriate change of variables  $n \mapsto (x, y)$ , into the slow-fast form:

$$\begin{cases} \frac{dx}{d\tau} = F(\tau, x, y) + \varepsilon H(\tau, x, y), \\ \frac{dy}{d\tau} = \varepsilon S(\tau, x, y). \end{cases}$$

In the above system, we are implicitly assuming that the fast process, now represented by  $F(\tau, x, y)$ , is conservative for the slow variables  $y$ . The next step in the reduction procedure consists in considering alone the dynamics associated to the fast process. In other words, we first consider the situation where  $\varepsilon = 0$ . Two additional assumptions are taken into account, the system is A.A. and the limit system associated to the fast process,  $dx/d\tau = \bar{F}(x, y)$ , possesses hyperbolically asymptotically stable equilibria,  $x^*(y)$ , for each fixed value of the slow variables  $y$ . Roughly speaking, we are considering those events occurring at the fastest scale as being instantaneous with respect to the slower ones. Thus, substituting equilibria  $x^*(y)$  into the equation for  $y$  we obtain the reduced, aggregated, system

$$\frac{dy}{dt} = \bar{S}(x^*(y), y)$$

where the effect of the fast dynamics is summarized by the parameters included in the expressions of the fast equilibria.

The study of the asymptotic behavior of the reduced system together with the fast equilibria allows to know the asymptotic behavior of the original system. The precise assumptions to be met, in order to ensure that the whole procedure is justified, are collected in Theorem 6. This theorem follows directly from the results provided in Hoppensteadt (1966, 1993, 2010).

The presented reduction method justify on theoretical grounds what is an implicit common practice: decoupling processes that act at different time scales which are certainly coupled. To illustrate the method, two different applications have been developed. The first one is described by system (4). In a two vessels gradostat, the dynamics of a nutrient and a primary producer (PP) are considered. This nutrient–PP system is coupled to a population consumer in the second vessel, feeding on the primary producer. Furthermore, we assume that demographic processes associated to the consumer are slow with respect to those associated to the nutrient and the PP. System (4) is autonomous, but solving it for a new variable turn it into an A.A. system. The equation for the consumer population reflects the fact that its resource availability is changing with time depending on primary producers concentration. The result of the reduction method shows us that the consumers dynamics can be approximated by a simpler model, where resource availability is taken to be constant.

This simplification can be very useful in many other situations. For instance, for some species, the amount of available resources has a continuous effect on fecundity while, for other species, there is a threshold effect because individuals must accumulate a given amount of resource before reproduction. In Dubreuil et al. (2006) for instance, a hawk–dove model with demography involving two time scales is analyzed, by taking into account these continuous/threshold effects. The authors consider a constant amount of resource. The application of the reduction method would permit, with the same effort, to study the influence of a variable resource provided that it tends to a constant value.

Another interesting application has to do with A.A. epidemic models, which importance is revealed in Castillo-Chavez and Thieme (1994). Autonomous ecoepidemic models with two time scales have been introduced in Auger et al. (2009). A predator–prey slow dynamics coupled to a fast epidemic process was analyzed. The same type of community model with an A.A. epidemic process would be susceptible of being studied with the help of the reduction technique.

The second application is presented in system (6). In a gradostat with two vessels, we consider two competing species for which all demographic parameters are affected by the concentration of a pollutant. The transference of the pollutant and the movements between vessels of individuals of both species are considered faster than demographic changes. This is also a schematic setting of many other situations; the pollutant can be interpreted more generally as a control factor. Solving system (6) with respect to the pollutant concentrations variables leads to an A.A. system, to which the reduction method applies. In order to bring the system into the slow–fast form, we use the global abundances of competing species as slow variables. The aggregated system turns out to be a classical Lotka–Volterra competition model. Theorem 6 allows to export the different outputs of a classical competition model to the model in (6) via the fast equilibria, which fix long term individual distributions between vessels together with asymptotic pollutant concentrations.

In this work, we have only dealt with two time scale systems, for which both the fast and the slow processes are assumed to be A.A. In Marva et al. (2012a,b,c) the authors addressed the approximate aggregation of slowly varying periodic systems with two time scales. A procedure analogous to the one presented above was developed for systems in which the fast and the slow processes are periodic with a common period. This period was of the order of magnitude as the slow time scale. We point out that there is no more difficulty in applying approximate aggregation techniques to models with two time scales and combining both A.A. terms with slowly varying periodic terms.

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#### Appendix A. Asymptotically autonomous systems and quasistatic-state approximation for nonlinear initial-value problems

This section is devoted to the mathematical justification of the approximate reduction technique presented in Section 3, which is then applied to analyze different population models.

We first introduce precise definitions of elements related to the asymptotically autonomous concept.

**Definition.** A continuous function  $A : (t_0, \infty) \times D \rightarrow D$  with  $(t_0, \infty) \times D \subset \mathbb{R} \times \mathbb{R}^N$ , is said to be asymptotically autonomous, if there exists a continuous function  $\bar{A} : D \rightarrow D$  such that the limit

$$\lim_{t \rightarrow \infty} A(t, z) = \bar{A}(z) \tag{A.1}$$

exists and it is locally uniform, that is, uniform on compact sets of  $D$ . If function  $A$  is asymptotically autonomous then the nonautonomous system of ordinary differential equations

$$z' = A(t, z)$$

is also said to be *asymptotically autonomous*, being its associated *limit system* the autonomous system

$$z' = \bar{A}(z).$$

The reduction technique presented in Section 3 relies on the results on quasistatic-state approximation for nonlinear initial-value problems, due to Hoppensteadt (1966, 1993, 2010). Hoppensteadt's results are dimension reduction results that allow us to extend approximate aggregation methods for autonomous two time scale systems (Auger et al., 2008, 2012) to nonautonomous ones.

Approximate aggregation methods for two time scale autonomous ode systems take the general form

$$\frac{dz}{d\tau} = v(z) + \varepsilon w(z), \tag{A.2}$$

where  $v, w : \mathbb{R}^p \rightarrow \mathbb{R}^p$  are smooth functions representing the *fast* and *slow* processes,  $z \in \mathbb{R}^p$  is the state variables vector and  $\varepsilon$  is the positive constant close to zero accounting for the ratio between time scales. The nonautonomous version of system (A.2) is

$$\frac{dz}{d\tau} = v(\tau, z) + \varepsilon w(\tau, z), \tag{A.3}$$

We assume that system (A.3) can be written in the slow-fast form

$$\begin{cases} \frac{dx}{d\tau} = F(\tau, x, y) + \varepsilon H(\tau, x, y), \\ \frac{dy}{d\tau} = \varepsilon S(\tau, x, y). \end{cases} \tag{A.4}$$

where  $x$  and  $y$  represent the *fast* and the *slow variables*, respectively. There is no general rule describing the transformation  $n \mapsto (x, y)$ . The construction of general algorithms performing it still remains an unsolved problem. Fortunately, in some applications, the context gives a natural way to define the also called *global variables*  $y$  and, thus, to express system (A.3) in slow-fast form.

Introducing variable  $t = \varepsilon\tau$ , related to the slow time unit, and calling

$$\begin{aligned} f(t, x, y, \varepsilon) &= F\left(\frac{t}{\varepsilon}, x, y\right) + \varepsilon H\left(\frac{t}{\varepsilon}, x, y\right) \\ g(t, x, y, \varepsilon) &= S\left(\frac{t}{\varepsilon}, x, y\right) \end{aligned} \tag{A.5}$$

we transform system (A.4) into the following one which reduction is treated in Hoppensteadt (1966, 1993, 2010)

$$\begin{cases} \varepsilon \frac{dx}{dt} = f(t, x, y, \varepsilon), & x(t_0) = \xi_0 \\ \frac{dy}{dt} = g(t, x, y, \varepsilon), & y(t_0) = \eta_0 \end{cases} \tag{A.6}$$

with  $x \in \mathbb{R}^n, y \in \mathbb{R}^m$  and  $\varepsilon$  is a small positive parameter. We define the domain  $\hat{\Omega} = \Omega \times [0, \varepsilon_0]$  where  $\Omega = I \times B_R \times B_{R'}$ ,  $I = \{t : t_0 \leq t \leq T \leq \infty\}$ ,  $B_R = \{x \in \mathbb{R}^n : |x| \leq R\}$  and  $B_{R'} = \{y \in \mathbb{R}^m :$

$|y| \leq R'\}$ ,  $T$  and  $\varepsilon_0$  being positive constants. In what follows, the balls  $B_R$  and  $B_{R'}$  can be replaced by any sets that are diffeomorphic to them.

Hoppensteadt's results need the following hypotheses to hold:

**Hypothesis H1.** Functions  $f$  and  $g$  are  $C^2(\Omega)$  and any solution of the system (A.6) beginning in  $B_R \times B_{R'}$  remains there for  $t_0 \leq t \leq T$ .

Setting  $\varepsilon = 0$  in (A.6) we obtain the reduced problem:

$$\begin{cases} 0 = f(t, x, y, 0) \\ \frac{dy}{dt} = g(t, x, y, 0), & y(t_0) = \eta_0 \end{cases} \tag{A.7}$$

**Hypothesis H2.** There is a function  $x = \Phi(t, y)$  such that  $f(t, \Phi(t, y), y, 0) = 0$  for  $(t, y) \in I \times B_{R'}$ . Moreover  $\Phi \in C^2(I \times B_{R'})$  and  $\det(f_x(t, \Phi(t, y), y, 0)) \neq 0$  for  $(t, y) \in I \times B_{R'}$ .

**Hypothesis H3.** The system of equations

$$\frac{dX}{d\tau} = f(\alpha, X, \beta, 0) \tag{A.8}$$

has  $X = \Phi(\alpha, \beta)$  as an equilibrium for each  $(\alpha, \beta) \in I \times B_{R'}$  that is asymptotically stable uniformly in the parameters  $(\alpha, \beta) \in I \times B_{R'}$ , and the initial condition  $\xi_0$  is in the domain of attraction of the equilibrium  $\Phi(t_0, \eta_0)$  for system (A.8) with  $\alpha = t_0$  and  $\beta = \eta_0$ .

**Hypothesis H4.** The system of equations

$$\frac{dy_0}{dt} = g(t, \Phi(t, y_0), y_0, 0) \tag{A.9}$$

has a solution for  $t_0 \leq t < \infty$ , say  $y^*(t)$ , that it is uniformly asymptotically stable and  $\eta_0$  is in the domain of attraction of  $y^*(t)$ . If those hypotheses are met the following theorem applies.

**Theorem 5.** Let Hypotheses H1–H4 be satisfied and let  $y_0(t)$  be the solution of (A.9) for  $y_0(t_0) = \eta_0$ . Then, for sufficiently small values of  $\varepsilon$  the solution of problem (A.6),  $(x(t), y(t))$ , exists for  $t_0 \leq t < \infty$  and it satisfies

$$x(t) = \Phi(t, y_0(t)) + o(1), \quad y(t) = y_0(t) + o(1)$$

as  $\varepsilon \rightarrow 0^+$  uniformly on any interval of the form  $t_0 < t_1 \leq t < \infty$ .

**Proof.** The interested reader can find a sketch of the proof in Hoppensteadt (2010) and the complete proof in Hoppensteadt (1966).  $\square$

It is clear from (A.5) that the assumption of functions  $F, H, S$  being A.A. is crucial for the existence of the corresponding reduced system (A.6). The following theorem gives an easy to apply version of Theorem 5 for asymptotically autonomous systems of the form of system (A.4).

**Theorem 6.** Let us consider system (A.4) where functions  $F, H, S$  are asymptotically autonomous on  $\Omega = [t_0, \infty) \times \Omega_m$ , where  $\Omega_m = K_R \times K_{R'}$ ,  $K_R = \{x \in \mathbb{R}^{n-k} : |x| \leq R\}$  and  $K_{R'} = \{y \in \mathbb{R}^k : |y| \leq R'\}$ ;  $\bar{F}, \bar{H}, \bar{S}$  being their corresponding asymptotic limit functions. Let us assume:

- 1  $F, H, S \in C^2(\Omega)$ ,  $\bar{F}, \bar{H}, \bar{S} \in C^2(\Omega_m)$  and any solution of system (A.4) beginning in  $K_R \times K_{R'}$  remains there for  $t \in [t_0, \infty)$ .
- 2 There is a function  $x = \Phi(y) \in C^2(K_{R'})$  such that for any  $y \in K_{R'}$  the following hold:
  - (a)  $\bar{F}(\Phi(y), y) = 0$ .

(b) The real part of the eigenvalues of  $J_x \bar{F}(\Phi(y), y)$  is negative for all  $y \in K_R$ .

3 The system of equations, the so-called aggregated system,

$$\frac{d\bar{y}}{dt} = \bar{S}(\Phi(\bar{y}), \bar{y}) \quad (\text{A.10})$$

has an asymptotically stable solution  $y^*(t)$ .

Let  $(x^\varepsilon(t), y^\varepsilon(t))$ ,  $t = \varepsilon\tau$ , be the solution of system (A.4) for  $(x^\varepsilon(t_0), y^\varepsilon(t_0)) = (x_0, y_0)$ , with  $x_0$  and  $y_0$  in the domains of attraction, respectively, of the equilibrium  $\Phi(y_0)$  of system  $d\bar{x}/dt = \bar{F}(\bar{x}, y_0)$  and of  $y^*(t)$ . Then, for any  $\delta > 0$ , there exist  $\varepsilon_\delta > 0$  and  $t_\delta > t_0$  such that

$$|(x^\varepsilon(t), y^\varepsilon(t)) - (\Phi(y^*(t)), y^*(t))| < \delta,$$

for every  $\varepsilon \leq \varepsilon_\delta$  and every  $t \geq t_\delta$ .

**Proof.** We recall that for autonomous systems asymptotic stability is equivalent to uniform asymptotic stability in the sense of Hoppensteadt (see Hahn, 1967). On the other hand, conditions 1–3 in the theorem imply Hypotheses H1–H4. So, the proof is a direct consequence of Theorem 5.  $\square$

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