Reduction of slow-fast periodic systems: fast migrations in a predator-prey community

M. MARVÁ†, J.C. POGGIALE*, R.BRAVO DE LA PARRA†.
†Departamento de Matemáticas, Universidad de Alcalá.
28871, Alcalá de Henares, Spain
marcos.marva@uah.es, rafael.bravo@uah.es
*Laboratoire de Microbiologie, Geochimie et dEcologie Marines, UMR 6117,
Centre dOceanologie de Marseille (OSU), Universite de la Mediterranee, Case 901,
Campus de Luminy 13288 Marseille Cedex 9, France
Jean-Christophe.Poggiale@univmed.fr

This work deals with the approximate reduction of a non-autonomous two time scales ordinary differential equations system with periodic coefficients. We illustrate this technique with the analysis of a two patches periodic Lotka-Volterra predator-prey type model with a refuge for prey. Considering migrations between patches to be faster than local interaction allows us to study a three dimensional system by means of a two dimensional one.

1. Introduction.

The description of ecological systems in terms of mathematical models makes those latter to be complex and thus requiring some reduction to be analytically tractable. This complexity arises from the fact that a detailed model necessarily includes observations and processes each of them related to a specific scale. A simplification of this situation needs to translate model processes from one to another scale by transferring information between them, what it is called scaling. Hierarchy theory provides the conceptual framework of how processes and components of an ecological system interrelate and how they can be ordered ([8, 10]).

In mathematical terms a system including several interacting organization levels can be seen as a system with different time scales. Each organization level consists of interacting entities with their own dynamics, and those entities of a given level with strong or fast interactions can be grouped giving rise to the entities at next level. Mathematically the process of up-scaling consists in deriving global variables and their dynamics from the lower level based on the existence of different time scales. This is roughly done by considering those events occurring at the fastest scale as being instantaneous with respect to the slower ones, what entails a reduction of the number of variables and parameters needed to describe the evolution of the system at the upper level.

An example of this general framework are the so-called *aggregation methods* which study the relationship between a large class of two-time scales complex systems and their corresponding *aggregated* or reduced ones. A review on these methods in different mathematical settings with updated bibliography can be found in Ref. [1, 2]. Aggregation techniques are particularly well developed for autonomous ordinary differential equations, being their mathematical basis the Fenichel center manifold theorems [5] and the geometric singular perturbation theory [12, 13]. In short, an autonomous system of ordinary differen-

tial equations with two scales can be expressed in the following form

$$\frac{d\mathbf{n}}{d\tau} = \mathbf{f}(\mathbf{n}) + \epsilon \mathbf{s}(\mathbf{n}) \tag{1.1}$$

with state variables $\mathbf{n} = (n_1, \cdots, n_m)$, where $\mathbf{f} = (f_1, \cdots, f_m)$ and $\mathbf{s} = (s_1, \cdots, s_m)$ are sufficiently regular functions describing the fast and slow dynamics, respectively, and ϵ is the small positive parameter measuring the time scales ratio. To perform its approximate aggregation, system (1.1) is firstly converted into slow-fast form by means of an appropriate change of variables $\mathbf{n} \in \mathbb{R}^m \longrightarrow (\mathbf{x},\, \mathbf{y}) \in \mathbb{R}^{m-k} \times \mathbb{R}^k$:

$$\begin{cases} \dfrac{d\mathbf{x}}{d\tau} = \mathbf{F}(\mathbf{x}, \mathbf{y}) + \epsilon \mathbf{S}(\mathbf{x}, \mathbf{y}) \\ \dfrac{d\mathbf{y}}{d\tau} = \epsilon \mathbf{G}(\mathbf{x}, \mathbf{y}) \end{cases} \tag{1.2}$$

where $\mathbf{x}$ represents the fast variables and $\mathbf{y}$ the slow variables. Finding the transformation $\mathbf{n} \mapsto (\mathbf{x},\, \mathbf{y})$ which yields the slow-fast form (1.2) of system (1.1) could be a difficult task and the construction of general algorithms solving this problem is presently an active research line. On the other hand, in some applications, as we will see later, the context gives a natural way to define the so-called *global variables* $\mathbf{y}$ and thus to express system (1.1) in slow-fast form.

The reduction process now consists in taking $\epsilon = 0$ in the first equation of the slow-fast form ((1.2)), $d\mathbf{x}/d\tau = \mathbf{F}(\mathbf{x}, \mathbf{y})$, and assuming, for constant $\mathbf{y}$, that there exist asymptotically stable equilibria $\mathbf{x}^*(\mathbf{y})$, in building up an *aggregated system* for the global variables with the following form:

$$\frac{d\mathbf{y}}{dt} = \mathbf{G}(\mathbf{x}^*(\mathbf{y}), \mathbf{y}) \tag{1.3}$$

where $t = \epsilon\tau$ represents the slow time variable. Under certain hypotheses the asymptotic behaviour of system (1.1) can be studied through system (1.3).

The purpose of this work is showing how to extend these reduction techniques to systems of non-autonomous ordinary differential equations. These systems represent more realistic population models compared with autonomous ones due to the flexibility to include time-varying features of the environment (light, temperature, relative humidity or resources availability) as well as demographic characteristics of the involved populations (migrations or reproduction) which are usually subjected to daily or seasonal variations. A particular and very relevant case of non-autonomous system is the periodic one, which is frequently found as model of natural systems.

We develop in section 2 the approximate reduction of a general class of two time scales systems of periodic ordinary differential equations of the form:

$$\frac{d\mathbf{n}}{d\tau} = \mathbf{f}(\mathbf{n}) + \epsilon \mathbf{s}(\epsilon\tau, \mathbf{n}) \tag{1.4}$$

where function $\mathbf{s}$ is periodic in time. To our knowledge the only result of approximate aggregation of a non-autonomous system is found in [9]. In this work, the fast dynamics is considered non-autonomous and assumed to tend to stationary periodic solutions depending on global variables; averaging techniques together with the aforementioned Fenichel

center manifold theorems allow to proceed to the reduction of the system. There is no overlap with our results since we introduce periodic time dependent slow dynamics and we use Hoppensteadt theorems on singular perturbations [7] to justify the suggested reduction.

In Section 3 we illustrate the aggregation techniques developed in Section 2 applying them to a two patches prey-predator model: prey can migrate between the patch where predators are and a refuge, local predator-prey interactions are described through a particular form of Beddington-DeAngelis [3] functional response with periodic coefficients, and, finally, prey migrations are assumed to be fast when compared with predator-prey interactions. We obtain the reduced system and study with its help the asymptotic behaviour of solutions of the initial system. Section 4 is devoted to conclusions and an appendix containing a proof completes the paper.

2. Reduction theorem.

In this section we present the reduction of system (1.4), $d\mathbf{n}/d\tau = \mathbf{f}(\mathbf{n}) + \epsilon\mathbf{s}(\epsilon\tau, \mathbf{n})$, which slow part depends on time at the slow time scale. We firstly suppose that (1.4) admits a slow-fast form:

$$\begin{cases} \dfrac{d\mathbf{x}}{d\tau} = \mathbf{F}(\mathbf{x}, \mathbf{y}) + \epsilon\mathbf{S}(\epsilon\tau, \mathbf{x}, \mathbf{y}) \\ \dfrac{d\mathbf{y}}{d\tau} = \epsilon\mathbf{G}(\epsilon\tau, \mathbf{x}, \mathbf{y}) \end{cases} \tag{2.1}$$

where $(\mathbf{x}, \mathbf{y}) \in \mathbb{R}^{m-k} \times \mathbb{R}^k$. The goal of this section is applying the results in Hopppensteadt [7] by imposing mild assumptions on $\mathbf{F}$, $\mathbf{S}$ and $\mathbf{G}$, so that system (1.4) can be studied through a reduced system. For this purpose, we make appear the slow time variable $t = \epsilon\tau$, obtaining:

$$\begin{cases} \epsilon\dfrac{d\mathbf{x}}{dt} = \mathbf{F}(\mathbf{x}, \mathbf{y}) + \epsilon\mathbf{S}(t, \mathbf{x}, \mathbf{y}) \\ \dfrac{d\mathbf{y}}{dt} = \mathbf{G}(t, \mathbf{x}, \mathbf{y}) \end{cases} \tag{2.2}$$

which, letting $\epsilon = 0$, yields the following system:

$$\begin{cases} 0 = \mathbf{F}(\mathbf{x}, \mathbf{y}), \\ \dfrac{d\mathbf{y}}{dt} = \mathbf{G}(t, \mathbf{x}, \mathbf{y}) \end{cases} \tag{2.3}$$

We find in system (2.3) the key to decouple slow and fast dynamics of system (2.1) and to derive the reduced system. Solving for $\mathbf{x}$, in terms of $\mathbf{y}$, the first equation in (2.3), i.e., finding $\mathbf{x}^*(\mathbf{y})$ such that $0 = \mathbf{F}(\mathbf{x}^*(\mathbf{y}), \mathbf{y})$, allows to obtain, by substitution in the second equation in (2.3), a reduced system for variables $\mathbf{y}$:

$$d\mathbf{y}/dt = \mathbf{G}(t, \mathbf{x}^*(\mathbf{y}), \mathbf{y})$$

which play the role of *aggregated system* and contains the information on the asymptotic behaviour of system (1.4) provided that hypotheses in the next theorem are met.

The following theorem summarizes the previous digression. From now on, we note

$$I := [t_0, +\infty) \qquad S_R := \left\{(\mathbf{x}, \mathbf{y}) \in \mathbb{R}^{m-k} \times \mathbb{R}^k;\ \|(\mathbf{x}_0, \mathbf{y}_0) - (\mathbf{x}, \mathbf{y})\| \leq R\right\}$$

where $(\mathbf{x}_0, \mathbf{y}_0)$ are the initial values of system (2.1). Finally, consider the sets

$$\mathcal{K} := \{d : [0, \infty) \to [0, \infty);\ d(0) = 0,\ \text{strictly increasing and continuous}\},$$

$$\mathcal{S} := \{\sigma : [0, \infty) \to [0, \infty);\ \lim_{t\to\infty} \sigma(t) = 0,\ \text{strictly decreasing and continuous}\}.$$

Theorem 2.1. *Consider system* (2.1)*, where* $\mathbf{F}$, $\mathbf{S}$, $\mathbf{G} \in \mathcal{C}^2$ *and* $\mathbf{S}$, $\mathbf{G}$ *are periodic functions of time. Let us note* $S|_{R_y}$ *the projection of* $S|_R$ *on* $\mathbb{R}^k$*. Assume that*

(C1) There exists a continuum of equilibria $\mathbf{x}^*(\beta)$*,* $\beta \in S|_{R_y}$ *for system (known as the boundary layer system)*

$$\frac{d\mathbf{x}}{ds} = \mathbf{F}(\mathbf{x}, \beta), \qquad \beta \in S|_{R_y}, \tag{2.4}$$

such that the real part of the eigenvalues of $J_{\mathbf{x}}\mathbf{F}(\mathbf{x}^*(\beta))$ *is negative* $\forall \beta \in S|_{R_y}$ *(where* J *stands for the Jacobian matrix).*

(C2) The aggregated system

$$\begin{cases} \dfrac{d\mathbf{y}}{dt} = \mathbf{G}(t, \mathbf{x}^*(t, \mathbf{y}), \mathbf{y}), \\ \mathbf{y}(t_0) = \mathbf{y}_0, \end{cases} \tag{2.5}$$

where $\mathbf{x}^*$ *is that of condition (C1), has a solution* $\mathbf{y}^*(t)$ *defined for all* $t \in I$ *which is uniformly-asymptotically stable. We mean that for any other solution* $\Phi(t, t_0, \bar{\mathbf{y}}_0)$ *of system* (2.5)*, there exist functions* $d \in \mathcal{R}$ *and* $\sigma \in \mathcal{S}$ *such that*

$$\|\mathbf{y}^*(t, t_0, \mathbf{y}_0) - \Phi(t, t_0, \bar{\mathbf{y}}_0)\| \leq d\left(\|\mathbf{y}_0 - \bar{\mathbf{y}}_0\|\right) \sigma(t - t_0). \tag{2.6}$$

Then, there exists $R > 0$ *such that for each* $\epsilon > 0$ *small enough and each* $(\bar{\mathbf{x}}_0, \bar{\mathbf{y}}_0) \in S_R$ *the corresponding solution* $(\mathbf{x}_\epsilon(t, t_0, \bar{\mathbf{x}}_0),\ \mathbf{y}_\epsilon(t, t_0, \bar{\mathbf{y}}_0))$ *of the original system* (2.1) *verifies*

$$\lim_{\epsilon\to 0} (\mathbf{x}_\epsilon(t, t_0, \bar{\mathbf{x}}_0),\ \mathbf{y}_\epsilon(t, t_0, \bar{\mathbf{y}}_0)) = (\mathbf{x}^*(\mathbf{y}^*(t)), \mathbf{y}^*(t))$$

uniformly on closed subset of $[t_0, \infty)$.

Proof.– Hoppensteadt's theorem is a general one and deals with systems of the form

$$\begin{cases} \epsilon \dfrac{d\mathbf{x}}{dt} = \varpi(t, \mathbf{x}, \mathbf{y}, \epsilon), \\ \dfrac{d\mathbf{y}}{dt} = \varphi(t, \mathbf{x}, \mathbf{y}, \epsilon). \end{cases} \tag{2.7}$$

Keeping in mind the precise form of system (2.2)

$$\begin{cases} \epsilon \dfrac{d\mathbf{x}}{dt} = \mathbf{F}(\mathbf{x}, \mathbf{y}) + \epsilon \mathbf{S}(t, \mathbf{x}, \mathbf{y}), \\ \dfrac{d\mathbf{y}}{dt} = \mathbf{G}(t, \mathbf{x}, \mathbf{y}), \end{cases}$$

and the fact that $\mathbf{F}$, $\mathbf{S}$, $\mathbf{G}$ are periodic functions of t, it is straightforward checking that Theorem 2.1 fulfills the hypothesis if the main Theorem in [7].

■

Remark 2.1. In condition (C1) we have assumed the existence of a continuum of equilibria $\mathbf{x}^*(\beta)$, $\forall\beta \in S|_{R_y}$, of system (2.4). Consider that there exist $\mathbf{x}_1^*(\beta)$ and $\mathbf{x}_2^*(\beta)$, such that $\mathbf{F}(\mathbf{x}_i^*(\beta), \beta) = 0$ for $i = 1, 2$, $\beta \in S|_{R_y}$ and that $\mathbf{x}_1^*(\bar{\beta}) \neq \mathbf{x}_2^*(\bar{\beta})$ for certain $\bar{\beta} \in S|_{R_y}$; that is, there exist two different continuum of such an equilibria. Then it is needed that $\mathbf{x}_1^*(\beta) \neq \mathbf{x}_2^*(\beta)$ $\forall\beta \in S|_{R_y}$ for theorem 2.1 to hold.

Remark 2.2. If functions $\mathbf{S}(t, \cdot, \cdot)$, $\mathbf{G}(t, \cdot, \cdot)$ were not periodic functions of time, the following regularity conditions are needed:

(C3) The following regularity conditions hold
- (a) $\mathbf{F}$, $\mathbf{S}$, $\mathbf{G}$, $\mathbf{F_x} + \epsilon\mathbf{S_x}$, $\mathbf{F_y} + \epsilon\mathbf{S_y}$, $\mathbf{F}_t + \epsilon\mathbf{S}_t$, $\mathbf{G_x}$, $\mathbf{G_y} \in \mathcal{C}(I \times S|_R \times [0, \epsilon_0))$, for certain $\epsilon_0 > 0$.
- (b) Function $\mathbf{G}$ is continuous at $\mathbf{x}^*(\mathbf{y})$ uniformly in $(t, \mathbf{y}) \in I \times S|_{R_\mathbf{y}}$.
- (c) Function $\mathbf{F} + \epsilon\mathbf{G}$ is continuous at $\epsilon = 0$ uniformly in $(t, \mathbf{x}, \mathbf{y}) \in I \times S|_R$. Moreover $\mathbf{F}$, $\mathbf{F}_t$, $\mathbf{F_x}$, $\mathbf{F_y}$ are bounded on $I \times S|_{R_\mathbf{y}}$

Corollary 2.1. *The existence of a bounded compact simply connected positively invariant region $\mathcal{R}$ for system* (2.5) *implies the existence of a periodic solution for system* (2.5).

Once we have a periodic solution for the aggregated system, checking condition (2.6) could be difficult. In this sense, the following result provide us with easy-to-check conditions

Corollary 2.2. *Assume that the aggregated system* (2.5) *posseses a periodic solution* $\mathbf{y}^*(t)$. *Consider the linearization of system* (2.5) *around* $\mathbf{y}^*$

$$\mathbf{z}' = \mathbf{G_y}(t, \mathbf{x}^*(\mathbf{y}^*), \mathbf{y}^*)\mathbf{z}. \tag{2.8}$$

Then, any of the following conditions assures that $\mathbf{y}^*(t)$ *is uniformly asymptotically stable in the sense of condition (C2):*

(1) The characteristic multipliers of system (2.8) *are in modulus less than one.*
(2) Condition (2.6) *holds for solution* $\mathbf{y}^*(t)$ *of system* (2.8).

Proof.– It follows from the considerations done at Section 4.2 (in particular, Theorem 4.2.1.) in [4].

■

3. Periodic predator-prey model with fast migrations.

This section begins with the construction of an spatially distributed two time scales predator-prey model with functional response of DeAngelis type [3]. Then, a reduced model is derived to simplify the study of the original one. After doing so, we perform a detailed analysis of the aggregated system.

3.1. *Construction and reduction of the system.*

We consider a predator-prey model in a two patches environment. Prey population at patch $i = 1, 2$ is noted by n_i. Prey can migrate from patch i at constant rate m_i. Predators p stay confined at the second region. Migrations are considered to be much faster than local dynamics which, in addition, are supposed to be periodic functions of time. The first patch is a refuge for prey, where its density evolves under a logistic growth law. In the second patch we let prey and predators interact. These interactions are described by a classical predator-prey system with intra-specific competition for prey and functional response given by

$$f_1(t, n_2, p) = \frac{a(t)\, n_2}{1 + b(t)\, n_2 + c(t)\, p} \tag{3.1}$$

where a measures the effect of capture rate, b stands for the time used for processing each capture (handling time) and, finally c is the time elapsed engaging with other predators. See DeAngelis [3] (where all coefficients were considered to be constant) and [11]. Therefore, the complete interaction term is

$$f_1(t, n_2, p)p = \frac{a(t)n_2 p}{1 + b(t)n_2 + c(t)p} \tag{3.2}$$

and assuming $b = 0$ (i.e., considering the time used for processing each capture to be negligible), it becomes

$$f_1(t, n_2, p)p = \frac{a(t)n_2 p}{1 + c(t)p}. \tag{3.3}$$

We let $t = \epsilon\tau$, meaning that the coefficients describing the interactions slowly change with τ; that is, these coefficients evolve at the slow time scale. All those settings are represented by means of the following system of non-autonomous ordinary differential equations:

$$\begin{cases} \dfrac{dn_1}{d\tau} = -m_1 n_1 + m_2 n_2 + \epsilon r_1(\epsilon\tau) n_1 \left(1 - \dfrac{n_1}{K_1(\epsilon\tau)}\right), \\[2ex] \dfrac{dn_2}{d\tau} = m_1 n_1 - m_2 n_2 + \epsilon \left(r_2(\epsilon\tau) n_2 \left(1 - \dfrac{n_2}{K_2(\epsilon\tau)}\right) - \dfrac{\phi_2(\epsilon\tau)\, n_2}{1 + c(\epsilon\tau)p}\, p\right), \\[2ex] \dfrac{dp}{d\tau} = \epsilon \left(-\lambda_3(\epsilon\tau)p + \dfrac{\phi_3(\epsilon\tau)\, n_2}{1 + c(\epsilon\tau)p}\, p\right), \end{cases} \tag{3.4}$$

where the functions r_j, λ_3, c, ϕ_{j+1}, $K_j \in \mathcal{C}^0$, for $j = 1, 2$, are positive, bounded away from zero and periodic with the same period T. These functions depend on the slow unit time $t = \epsilon\tau$. On the other hand, ϵ is a small positive parameter representing the ratio between the time scales. As usual, r_i (i=1,2) and λ_3 stand for the respective net growth rates, K_i (i=1,2) is the carrying capacity, ϕ_i (i=1,2) measures the effect of captures in prey and predator populations and c is the time elapsed engaging with other predators. We will set $c = 1$, so that we keep the effect of interferences between predators but simplify the system (which already depends on many parameters).

It is apparent that, at $\epsilon = 0$, there exists an stable manifold of equilibria for the fast dynamics which are not asymptotically stable. Thus, condition (C1) fails. In this context, according with [1], using the global variable

$$p(\tau) = n_1(\tau) + n_2(\tau), \tag{3.5}$$

allow us to write system (3.4) in the appropriate slow fast form. Let us now introduce frequencies as

$$\nu_i(\tau) = p_i(\tau)/p(\tau), \qquad i = 1, 2. \tag{3.6}$$

In terms of the frequencies, system (3.4) reads as follows

$$\begin{cases} \epsilon \dfrac{d\nu_1}{dt} = m_2 - (m_1 + m_2)\nu_1 + \epsilon(1-\nu_1)\left[r_1(t)\left(1 - \dfrac{\nu_1\, p}{K_1(t)}\right)\nu_1 - r_2(t)\left(1 - \dfrac{(1-\nu_1)\, p}{K_2(t)}\right) + \dfrac{\phi_2(t)p}{1+p}\right], \\ \dfrac{dn}{dt} = \left[r_1(t)\left(1 - \dfrac{\nu_1\, n}{K_1(t)}\right)\nu_1 + r_2(t)\left(1 - \dfrac{(1-\nu_1)\, n}{K_2(t)}\right)(1-\nu_1) - \dfrac{\phi_2(t)(1-\nu_1)p}{1+p}\right] n, \\ \dfrac{dp}{dt} = \left[-\lambda_3(t) + \dfrac{\phi_3(t)(1-\nu_1)\, n}{1+p}\right] p, \\ n_1(t_0) = n_{10},\ n_2(t_0) = n_{20},\ p(t_0) = p_0 \end{cases} \tag{3.7}$$

provided $t = \epsilon\tau$. The following result is straightforward:

Lemma 3.1. *Consider the boundary layer problem* (2.4) *associated with system* (3.7)*. It holds that*

$$\nu_1^* := \frac{m_2}{m_1 + m_2} = \nu_1^*(n, p), \tag{3.8}$$

fulfills condition (C1) in Theorem 2.1.

From now on, we note $z' = dz/dt$. Thus, the *aggregated system* reads:

$$\begin{cases} n' = (a(t) - b(t)n)\, n - \dfrac{c(t)\, n}{1+p}\, p, \\ p' = -\lambda(t)p + \dfrac{f(t)\, n}{1+p}\, p, \end{cases} \tag{3.9}$$

where

$$\begin{cases} a(t) = r_1(t)\nu_1^* + r_2(t)\nu_2^*, \quad b(t) = \dfrac{r_1(t)(\nu_1^*)^2}{K_1(t)} + \dfrac{r_2(t)(\nu_2^*)^2}{K_2(t)}, \\ \qquad c(t) = \phi_2(t)\nu_2^*, \qquad \lambda(t) = \lambda_3(t), \qquad f(t) = \phi_3(t)\nu_2^*. \end{cases} \tag{3.10}$$

3.2. *Analysis of the aggregated system.*

We carry on with the study of system (3.9). For further purposes, we recall that the functions defined in (3.10) are periodic, positive and bounded away from zero. Thus, achieve

strictly positive minimum and maximum, which we will note as

$$\begin{cases} a_L \leq a(t) \leq a_M & b_L \leq b(t) \leq b_M \\ c_L \leq c(t) \leq c_M & \lambda_L \leq \lambda(t) \leq \lambda_M \\ f_L \leq f(t) \leq f_M \end{cases} \tag{3.11}$$

System (3.9) always admits the trivial solution $(n(t), p(t)) = (0, 0)$ for all $t \geq t_0$. Moreover, if we let $p(t) = 0$, then system (3.9) simplifies in

$$n' = (a(t) - b(t)n)\, n, \qquad n(t_0) = n_0, \tag{3.12}$$

which was studied in [6]. In this paper, it was shown that if $a(t) > 0$ and $b(t) > 0$ are periodic functions with common period T, then there exists an unique positive periodic solution $n_0^*(t)$ for (3.12) which is globally asymptotically stable. We will refer to $(n_0^*(t), \mathbf{0})$ as the semi-trivial solution of system (3.9). Later on, we will relate the existence of an asymptotically stable positive periodic solution of problem (3.9) with the stability of the semi-trivial solution. Both positive semi-axes are invariant sets for system (3.9).

Proposition 3.1. *Let us assume that condition*

$$0 < \frac{\lambda_M}{f_L} < \frac{a_L}{b_M} \tag{3.13}$$

holds. Then, there exist $\epsilon_0 > 0$ and $\delta > 0$ such that for each $\epsilon \in (0, \epsilon_0)$

$$\lim_{\epsilon \to 0} (n_1^\epsilon(t), n_2^\epsilon(t), p(t)) = (\nu_1^* n^*(t), (1 - \nu_1^*) n^*(t), p^*(t))$$

uniformly on closed subintervals of $[t_0, \infty)$, where ν_1^* is that of (3.8)*, $(n^*(t), p^*(t))$ is a positive periodic solution of the aggregated system* (3.9) *and $(n_1^\epsilon(t), n_2^\epsilon(t), p(t)^\epsilon(t))$ is the solution of* (3.4) *with initial values $(\bar{n}_{10}, \bar{n}_{,20}, \bar{p})$ such that*

$$\|(\bar{n}_{10}, \bar{n}_{20}, \bar{p}) - (n_{10}, n_{20}, p_0)\| < \delta.$$

Proof.– The proof is decomposed in several steps. First, the following result will be needed in the proof:

Lemma 3.2. *Let $b_{ij}(t) > 0$, where $i, j = 1, 2$, be strictly positive periodic functions with period T. The, the zero solution of system*

$$\begin{cases} z_1' = -b_{11}(t) z_1 - b_{12}(t) z_2 \\ z_2' = \ \ b_{21}(t) z_1 - b_{22}(t) z_2 \end{cases}$$

is asymptotically stable uniformly in the sense of Hoppensteadt.

Proof.– See the Appendix

Next, we will find a convex invariant region $\mathcal{R}$ for system (3.9). Applying a fixed point theorem yields the existence of at least a positive periodic solution for system (3.9) within $\mathcal{R}$. Finally, we will show that such a solution is uniformly-asymptotically stable in the sense of Hoppensteadt.

Step 1. Existence of a positive periodic solution.
With the help of bounds (3.11), direct calculations yield curves bounding regions of the fist quadrant where the sign of n' and p' are constant. Namely

$$\begin{cases} n < \dfrac{1}{b_M}\left[a_L - c_M \dfrac{p}{1+p}\right] \Rightarrow 0 < n' \\ n > \dfrac{1}{b_L}\left[a_M - c_L \dfrac{p}{1+p}\right] \Rightarrow 0 > n' \\ p < \dfrac{f_L}{\lambda_M} n - 1 \Rightarrow 0 < p' \\ p > \dfrac{f_M}{\lambda_L} n - 1 \Rightarrow 0 > p' \end{cases} \tag{3.14}$$

Figure 1 shows such a curves.

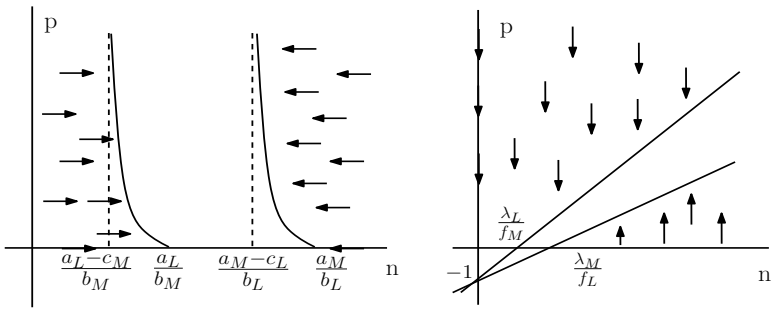

Fig. 1. Left and right: regions where the sign of n' and p' is constant. The curves are noted, from left to right, $n'_+(n)$, $n'_-(n)$, $p'_-(n)$ and $p'_+(n)$.

Depending on the relative position of the nulclines of the bounding equations (3.14) we can find different scenarios. We seek for a positively invariant, convex region $\mathcal{R}$ bounded away from the axes. We will build a rectangular region $\mathcal{R}$ thus, we shall find $r_i \in \mathbb{R}$, $i = 1, \cdots, 4$ such that $\mathcal{R} := [r_1, r_2] \times [r_3, r_4]$. Keeping in mind that $n = (a_L - c_m)/b_M$ is an asymptotic (vertical) line to $n'_+(n)$, we can place r_1 anywhere in $(0, (a_L - c_m)/b_M)$. Moreover, as $n'_+(n) < n'_-(n) < a_M/b_L$, we can choose $r_2 \geq a_M/b_L$. On the other hand, we recall that $0 < \lambda_M/f_L < a_L/b_M$ holds. Thus, the curve $p = p'_+(n)$ meets the vertical line $n = a_L/b_M$ at $\bar{p} > 0$ and we can let $r_3 \in (0, \bar{p})$. Finally, as $p'_-(n) > p'_+(n)$ for $n \geq 0$, if $\bar{\bar{p}}$ is the intersection between $p'_-(n)$ and $n = a_M/b_L$, choosing $r_4 \geq \bar{\bar{p}}$ yields $\mathcal{R}$. We have found lower and upper bounds for the vertex $r_i \in \mathbb{R}$, $i = 1, \cdots, 4$ of $\mathcal{R}$. From now on, we will refer to $\mathcal{R}$ as the minimal of such a rectangles. From the bounds for the derivatives of $(n(t), p(t))$ given by equation (3.14), the comparison theorem and its construction, it follows that $\mathcal{R} = [r_1, r_2] \times [r_3, r_4]$ is the region we where looking for. Figure 2 shows an rectangular closed invariant region $\mathcal{R}$.

Let us consider the T-operator $\varphi_T : \mathcal{R} \to \mathcal{R}$ defined by

$$\varphi_T(n, p) = \varphi(T, 0, n, p)$$

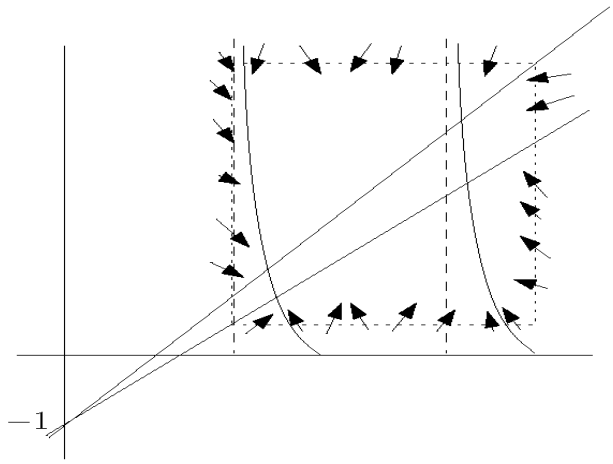

Fig. 2. The invariant region $\mathcal{R}$.

which maps each initial value on the region $\mathcal{R}$ into the value at time $t = T$ of the solution of problem (3.9) which starts at the initial values (n, p), namely $\varphi(T, 0, n, p)$. This is a continuous map and $\mathcal{R}$ is convex (it is rectangular) and by the Brouwer's fixed point theorem this operator has a fixed point, which means that there exists a solution $\mathbf{y}^*$ of the problem (3.9) such that

$$\varphi(T, 0, n, p) = \varphi(0, 0, n, p)$$

that is, the (3.9) problem has, at least, a positive periodic solution, which is globally defined.

Step 2. The periodic solution is stable in the sense of condition (C2).
In order to assure the attraction of the periodic solution, according to Corollary 2.2 we will study the stability of the zero solution of the variational problem of (3.9) at $\mathbf{y}^*$ (i.e., we linearize the problem at the periodic solution, see [4]). Thus, we will deal with the system

$$X' = A(t)X \tag{3.15}$$

where

$$A(t) = \begin{pmatrix} a(t) - 2b(t)n_0(t) - \dfrac{c(t)p_0(t)}{1+p_0(t)} & \dfrac{-c(t)n_0(t)}{(1+p_0(t))^2} \\ \dfrac{f(t)p_0(t)}{1+p_0(t)} & -\lambda(t) + \dfrac{f(t)n_0(t)}{(1+p_0(t))^2} \end{pmatrix} \tag{3.16}$$

and $\varphi(t) = (n_0(t), p_0(t))$ are the components of the periodic solution. Keeping in mind the fact that

$$\begin{cases} n_0'(t)/n_0(t) = a(t) - b(t)n_0(t) - \dfrac{c(t)p_0(t)}{1+p_0(t)} \\ p_0'(t)/p_0(t) = -\lambda(t) + \dfrac{f(t)n_0(t)}{1+p_0(t)} \end{cases}$$

the change of variables $y_1 = x_1/n_0$, $y_2 = x_2/p_0$ transforms the system (3.16) into

$$Y' = B(t)Y \tag{3.17}$$

where

$$B(t) = (b_{ij}(t)) = \begin{pmatrix} -b(t)n_0(t) & \dfrac{-c(t)p_0(t)}{(1+p_0(t))^2} \\ \dfrac{f(t)n_0(t)}{1+p_0(t)} & \dfrac{-f(t)p_0(t)n_0(t)}{(1+p_0(t))^2} \end{pmatrix}, \tag{3.18}$$

which is equivalent to (3.16). Applying Lemma 3.2 finishes the proof.

■

The following two results (Corollary 3.1 and Proposition 3.2) concern the aggregated system, but can not be translated to the general system. We include them by the shake of completeness.

Corollary 3.1. *All positive solutions of system* (3.9) *are bounded.*

Proof.– As the axes are invariant regions for system (3.9), this statement refers to solutions with positive initial values $(n(t_0), p(t_0)) = (n_0, p_0)$. Keeping in mind the construction of the invariant rectangle $\mathcal{R}$ (see step 1 in the proof of Proposition 3.1), if $n_0 \leq a_M$ and $p_0 \leq \bar{\bar{p}}$, then this Corollary holds. Other possible cases (i.e., if $n_0 > a_M$ or $p_0 > \bar{\bar{p}}$) are straightforward.

■

Proposition 3.2. *If condition* $0 < \dfrac{\lambda_M}{f_L} < \dfrac{a_L}{b_M}$ *holds, then there exists an unique* T*-periodic positive solution of problem* (3.9) *within region* $\mathcal{R}$.

Proof.– The proof follows an application of the topological degree. Consider the φ_T operator defined in the proof of the previous Proposition. Let us define

$$\begin{aligned} F := I - \varphi : \mathbb{R}^2_+ &\to \mathbb{R}^2_+ \\ (r,s) &\mapsto F(r,s) := (r - n(T,r,s),\ s - p(T,r,s)) \end{aligned}$$

where n and p stand for the solutions of the (P_0) problem such that $n(0) = r$ and $p(0) = s$. We already know that φ_T maps ∂R into Int$(\mathcal{R})$, therefore $F(r,s) \neq (0,0)$ for all $(r,s) \in \partial R$. Moreover, for $(r_1, s_1) \in$ Int(R) we define

$$N(r,s,\xi) := (r_1 + \xi\,[n(T,r,s) - r_1]\,;\ s_1 + \xi\,[p(T,r,s) - s_1])\,, \qquad (r,s) \in \bar{R}$$

As $N(r,s,0) = (r_1, s_1) \in$ Int(R), $N(r,s,1) = (n(T,r,s),\ p(T,r,s) \in$ Int(R) and R is convex, it is clear that

$$(r,s,) - N(r,s,\xi) \neq (0,0), \qquad \forall (r,s) \in \partial R,\ \ \xi \in [0,1].$$

Therefore, N establishes an admissible homotopy between

$$F(r,s) = (r,s) - N(r,s,0) \qquad \text{and} \qquad (r - r_1, s - s_1) = (r,s) - N(r,s,1)$$

and

$$d\left[F, R_2, 0\right] = d\left[(r - r_1, s - s_1), R_2, 0\right] = 1.$$

We must show that $|JF(P_0, p_0)| > 0$ for each positive T-periodic solution (n_0, p_0):

$$|JF(P_0, p_0)| = \begin{vmatrix} 1 - n_n'(T, n_0, p_0) & -n_p'(T, n_0, p_0) \\ -p_n'(T, n_0, p_0) & 1 - p_p'(T, n_0, p_0) \end{vmatrix}$$

and the eigenvalues of the matrix

$$\begin{pmatrix} n_n'(T, n_0, p_0) & n_p'(T, n_0, p_0) \\ p_n'(T, n_0, p_0) & p_p'(T, n_0, p_0) \end{pmatrix}$$

are the characteristic multipliers λ_1 and λ_2 of the aggregated system (3.9). We already know that such a solution is attractive, which implies that $|\lambda_i| < 1$ for $i = 1, 2$. Now, it is clear that

$$|JF(n_0, p_0)| = (1 - \lambda_1)(1 - \lambda_2) > 0,$$

which concludes with the proof of the uniqueness.

■

The following results concern the stability of the semi-trivial solution of the aggregated system which, in some cases, implies the exclusion (extinction) of predators at low population densities.

Proposition 3.3. *The semi-trivial solution* $(n_0^*, 0)$ *of the aggregated system* (3.9) *is asymptotically stable if*

$$\int_{t_0}^{t_0+T} \left(-\lambda(t) + f(t)n_0^*(t)\right) dt < 0 \tag{3.19}$$

Proof.– Linearizing the aggregated system (3.9) around the semi-trivial solution yields

$$\begin{pmatrix} x_1' \\ x_2' \end{pmatrix} = \begin{pmatrix} a(t) - 2b(t)n_0^*(t) & -c(t)n_0^*(t) \\ 0 & -\lambda(t) + f(t)n_0^*(t) \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} \tag{3.20}$$

This is a linear periodic system and we need calculate the Floquet exponents in order to study its stability. System (3.20) is a diagonal one and can be explicitly solved. The second equation in (3.20) is

$$x_2' = (-\lambda(t) + f(t)n_0^*(t))x_2$$

and its solution is given by

$$x_2(t) = x_2(t_0) \exp\left(\int_{t_0}^{t} -\lambda(s) + f(s)n_0^*(s)ds\right).$$

Replacing this expression into the first equation and solving it we get a fundamental system:

$$\Phi(t) = \begin{pmatrix} \exp\left(\int_{t_0}^{t} (a(s) - 2b(s)n_0^*(s))ds\right) & \Phi_{12}(t) \\ 0 & \exp\left(\int_{t_0}^{t} -\lambda(s) + f(s)n_0^*(s)ds\right) \end{pmatrix}$$

where $\Phi_{12}(t)$ is a complex expression. Moreover, the Floquet exponents are given by

$$\lambda_1 = \exp\left(\int_{t_0}^{t_0+T} (a(s) - 2b(s)n_0^*(s))ds\right) \qquad \lambda_2 = \exp\left(\int_{t_0}^{t_0+T} -\lambda(s) + f(s)n_0^*(s)ds\right)$$

On the one hand, $|\lambda_2| < 1$ because of condition (3.19). On the other hand, $|\lambda_1| < 1$ because $b(s)n_0^*(s) > 0$ and

$$\int_{t_0}^{t_0+T} (a(s) - b(s)n_0^*(s))ds = 0.$$

■

Proposition 3.4. *Let us assume that condition*

$$\frac{a_M}{b_L} < \frac{\lambda_L}{f_M}, \tag{3.21}$$

holds. Then, there exist $\epsilon_0 > 0$ *and* $\delta > 0$ *such that for each* $\epsilon \in (0, \epsilon_0)$

$$\lim_{\epsilon \to 0} (n_1^\epsilon(t), n_2^\epsilon(t), p^\epsilon(t)) = (\nu_1^* n_0^*(t), (1 - \nu_1^*)n_0^*(t), 0)$$

uniformly on closed subintervals of $[t_0, \infty)$*, where* ν_1^* *is that of* (3.8)*,* $(n_0^*(t), 0)$ *is the semi-trivial solution of the aggregated system* (3.9) *and* $(n_1^\epsilon(t), n_2^\epsilon(t), p(t))$ *is the solution of* (3.4) *with initial values* $(\bar{n}_{10}, \bar{n}_{,20}, \bar{p})$ *such that*

$$\|(\bar{n}_{10}, \bar{n}_{20}, \bar{p}) - (n_{10}, n_{20}, 0)\| < \delta.$$

Proof.– It follows from the proof of Proposition 3.3. Using the bounds (3.11) for the coefficients we get bounds for the solution

$$x_2^L(t) := x_2(t_0)e^{(-\lambda_M + f_L n_{0_L}^*)(t-t_0)} \leq x_2(t) \leq x_2(t_0)e^{(-\lambda_L + f_M n_{0_M}^*)(t-t_0)} =: x_2^M(t).$$

The fact that $\dfrac{a_L}{b_M} \leq n_0^*(t) \leq \dfrac{a_M}{b_L}$ finishes the proof.

■

Corollary 3.2. *The semi-trivial solution* $(n_0^*, 0)$ *is a global attractor for the aggregated system* (3.9) *if*

$$\frac{a_M}{b_L} < \frac{\lambda_L}{f_M}.$$

Proof.– We recall from the proof of Proposition 3.2 that $a_L/b_M \leq n_0^*(t) \leq a_M/b_L$ for all $t \geq 0$ and that $(n_0^*(t), 0)$ is uniformly asymptotically stable. Thus, there exists $\epsilon_0 > 0$ such that for each $0 < \epsilon < \epsilon_0$ every solution of (3.9) with initial values within

$$\mathcal{W}_\epsilon := [a_L/b_M - \epsilon,\, a_M/b_L + \epsilon] \times [0,\, \epsilon]$$

is attracted by the semi-trivial solution. Let ρ be a positive constant such that $0 < \rho < \min\{\epsilon, (a_L - c_M)/b_M\}$ and $n'_{+,\rho}(n) = n'_+(n) - \rho$. For a fixed ϵ, we note the region

bounded by the curves $n'_{+,\rho}(n)$ and $n = a_M/b_L$ by $\mathcal{Q}$ (including those points on the curves). Moreover, we define

$$\mathcal{Q}_2 := \mathcal{Q} \cup \mathcal{W}_\epsilon$$

$$\mathcal{Q}_1 = \left\{(n,p) \in \mathbb{R}^2;\, 0 < n < a_L/b_M;\, 0 < p\right\} \setminus \mathcal{Q}_2,$$

$$\mathcal{Q}_3 = \left\{(n,p) \in \mathbb{R}^2;\, a_M/b_L < n;\, 0 < p\right\} \setminus \mathcal{W}_\epsilon.$$

As $\lambda_L/f_M \geq a_M/b_L$, from equations (3.14) we notice that there exist constants positive δ_1 and δ_3 such that $n'(t) < -\delta_3 < 0$ in $\mathcal{Q}_3$ and $n'(t) > \delta_1 > 0$ in $\mathcal{Q}_1$. Thus, solutions starting in both regions $\mathcal{Q}_1$ and $\mathcal{Q}_3$ will leave them (and so, reach $\mathcal{Q}_2$ and stay in) after a transient time. The same reason implies that solutions starting within $\mathcal{Q}_2$ will remain in $\mathcal{Q}_2$. Moreover, there exits $\delta_2 > 0$ such that $p'(t) < -\delta_2 < 0$ in $\mathcal{Q}_2$. Thus, every positive solution $(n(t), p(t))$ in $\mathcal{Q}_2$ is strictly decreasing and

$$\lim_{t\to+\infty} (n(t), p(t)) \in \mathcal{W}_\epsilon,$$

which finishes the proof.

■

Corollary 3.3. *The semi-trivial solution of the aggregated system* (3.9) *is unstable if*

$$\frac{\lambda_M}{f_L} < \frac{a_L}{b_M}.$$

■

Conditions (3.13) and (3.21) state whether predator population is excluded or not. Nevertheless, these conditions do not cover all the possible cases. Thus, we turn out attention to the uncovered cases, namely, we consider that

$$\frac{a_L}{b_M} < \frac{\lambda_M}{f_L} \qquad \text{and} \qquad \frac{\lambda_L}{f_M} < \frac{a_M}{b_L}.$$

This cases can not be analyzed analytically. Numerical experiments show that, within this case, we can have either a positive solution (coexistence) or a semi-trivial omega limit (predators exclusion) for system (3.4). Thus, either coexistence or exclusion of predators population can happen. Let us illustrate this fact though the following numerical simulations.

Case 1: coexistence. - We consider a set of parameter (see next figure) which leads to condition:

$$\frac{\lambda_M}{f_L} > \frac{a_L}{b_M} \qquad \text{and} \qquad \frac{\lambda_L}{f_M} < \frac{a_M}{b_L}.$$

For these parameters, we represent, on the one hand, the state variables versus time showing that a positive periodic orbit exists and, on the other hand, a phase portrait illustrating the

positive periodic orbit. In addition we have included a comparison of the total prey/predator density simulated with the full and the aggregated model.

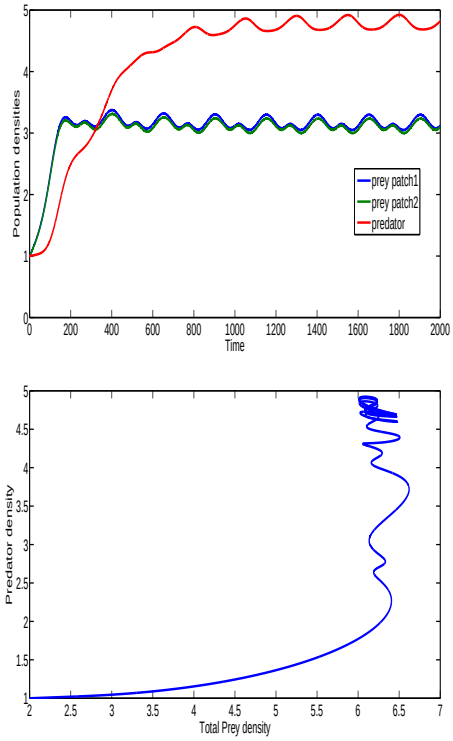

Fig. 3. Left: state variables vs time: a positive periodic orbit exists. Right: phase portrait of the aggregated model illustrating the positive periodic orbit. Parameter values $m_1 = 1$ $m_2 = 1$, $r_{1L} = 1$, $r_{2L} = 0.1$, $r_{1M} = 3$, $r_{2M} = 2.1$, $\phi_{2L} = 0.1$, $\phi_{3L} = 0.8 * \phi_{2L}$, $\phi_{2M} = 2.1$, $\phi_{3M} = \phi_{2M} * 0.8$, $\lambda_{3L} = 0.01$, $\lambda_{3M} = 1.01$, $T = 5$, $\epsilon = 0.02$, $K_{1L} = 5$, $K_{2L} = 1$,$K_{1M} = 9$, $K_{2M} = 5$,

Let us assume that there exists a positive solution for the aggregated system (3.9) for the parameter values listed above. We can go through step two in the proof of proposition 3.1 to ensure that, in fact, every positive periodic solution is uniformly-asymptotically stable. Thus, condition (2.6) in (C2) holds and Theorem 2.1 holds. The following simulation (keeping the parameter values in Figure 4) illustrates this fact:

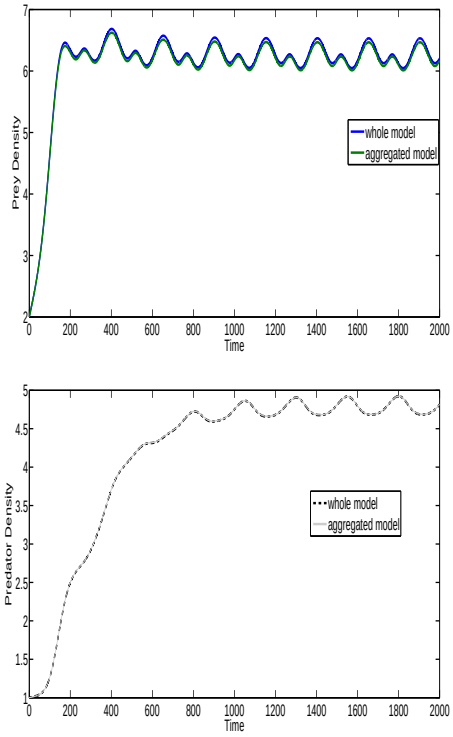

Fig. 4. Comparison of the total prey density (left) and total predator density (right) simulated with the full and the aggregated model. Parameter values are these of Figure 4

Case 2: predators exclusion. - We consider now the parameter set values in Figure 5, which yield:

$$\frac{\lambda_M}{f_L} > \frac{a_L}{b_M} \qquad \text{and} \qquad \frac{\lambda_L}{f_M} < \frac{a_M}{b_L}.$$

Again, for these parameter values, we represent the state variables in front of time showing that the predator can be excluded. On the other hand, the corresponding phase portrait illustrates the exclusion scenario. In this case, we could not establish analytically the stability of the semi-trivial. Nevertheless, the following simulation shows that results obtained with the parameter values stated in Figure 5 for the general and aggregated system are coherent:

4. Conclusions.

We have extended the approximate aggregation techniques for two time scales systems described by Auger *et al.* (see [1] and references therein) to non autonomous periodic cases. Namely, we consider non autonomous two time scales systems depending on the slow time unit. Instead of using Fenichel center manifold Theorems, our results are based upon a

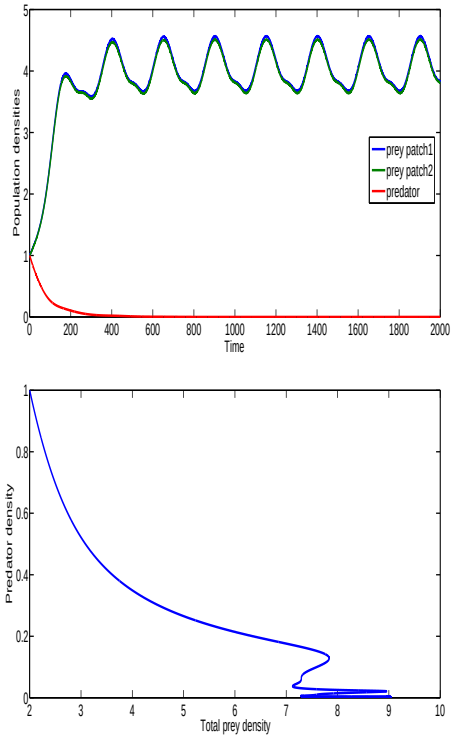

Fig. 5. Left: state variables vs time: prey permanence; predators extinction. Right: phase portrait of the aggregated model illustrating predators exclusion. Parameter values: $m_1 = 1$, $m_2 = 1$, $r_{1L} = 1$, $r_{2L} = 0.1$, $r_{1M} = 3$, $r_{2M} = 2.1$, $\phi_{2L} = 0.1$, $\phi_{3L} = 0.2 * \phi_{2L}$, $\phi_{2M} = 2.1$, $\phi_{3M} = 0.2 * \phi_{2M}$, $\lambda_{3L} = 0.6$, $\lambda_{3M} = 1.6$, $T = 5$, $\epsilon = 0.02$, $K_{1L} = 5$, $K_{2L} = 1$, $K_{1M} = 9$, $K_{2M} = 5$.

theorem due to F.C. Hoppensteadt [7] concerning singular perturbations on the infinite interval. This theorem is a general one and, as a counterpart, the corresponding hypothesis are rather restrictive and complicated to be checked. Nevertheless, as we have shown, when dealing with periodic systems the Hoppensteadt Theorem's hypothesis become much simpler, as collected in conditions (C1) and (C2). On the other hand, because of the nature of this theorem, we can translate results concerning only periodic uniformly-asymptotically stable solutions of the aggregated system to the general one.

With the help of these results, we have studied a two time scales spatially distributed predator prey system by means of a less dimensional (aggregated) one:

$$\begin{cases} n' = (a(t) - b(t)n)\, n - \dfrac{c(t)\, n}{1+p}\, p, \\ p' = -\lambda(t)p + \dfrac{f(t)\, n}{1+p}\, p. \end{cases}$$

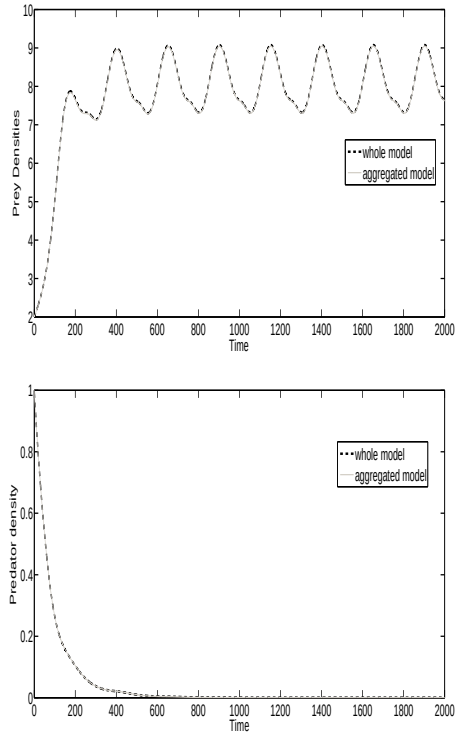

Fig. 6. Comparison of the total prey density (left) and total predator density (right) simulated with the full and the aggregated model. Parameter values are these stated in Figure 5.

Our results state thresholds for coexistence and predator's exclusion in terms of the relative shape of certain "vital parameters" of the aggregated system, namely, the maximum and the minimum of

$$\frac{a(t)}{b(t)} \qquad \text{and} \qquad \frac{\lambda(t)}{f(t)}. \tag{4.1}$$

Lets interpret the meaning of these quotients. In a non spatially distributed system, $a(t)/b(t)$ stands for the carrying capacity of the corresponding ecosystem. According to (3.10), it follows that

$$\frac{a(t)}{b(t)} = \frac{(r_1(t)\nu_1^* + r_2(t)\nu_2^*)K_1(t)K_2(t)}{r_1(t)(\nu_1^*)^2K_2(t) + r_2(t)(\nu_2^*)^2K_1(t)}.$$

which is the carrying capacity for the spatially distributed prey population when we consider fast migrations and periodic coefficients at each region. On the other hand,

$$\frac{\lambda(t)}{f(t)}$$

stands for the ratio between predator's mortality rate and benefits of captures for predators. Thus, we have stated conditions ensuring the existence of a coexistence state (condition

(3.13)) and the exclusion of predators at low population densities (condition (3.21)) in terms of (4.1). Summing up:

- There exists an attracting periodic coexistence state if $\dfrac{\lambda_M}{f_L} < \dfrac{a_L}{b_M}$.
- Predators die out at low population densities when $\dfrac{a_M}{b_L} < \dfrac{\lambda_L}{f_M}$.
- There exist a range of intermediate cases
$$\frac{\lambda_M}{f_L} > \frac{a_L}{b_M} \qquad \text{and} \qquad \frac{\lambda_L}{f_M} < \frac{a_M}{b_L}$$
which are indefinite meaning that both predators exclusion or coexistence can arise.

In the context of the system we are dealing with, coefficients $a(t)$, $b(t)$ and $f(t)$ depend on ν_1^*, which is related with prey migrations. In fact, from Corollary 3.2 and the definition of the coefficients (3.11), small changes in ν_1^* may entail a change in the stability of the semi-trivial solution of the aggregated system and thus, induce the extinction of predators at low predator population density.

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5. Appendix A: proof of Lemma 3.2.

We recall that $b_{ij}(t)$, for $i, j = 1, 2$, are periodic positive functions. Let us note the minimum and the maximum of each $b_{ij}(t)$, for $i, j = 1, 2$, as $0 < b_{ij}^L$ and $0 < b_{ij}^M$, respectively. Before proceeding, we recall a simple fact.

Remark 5.1. Consider system

$$Z'(t) = BZ(t), \tag{5.1}$$

where B is given by

$$\begin{pmatrix} -b_{11} & -b_{12} \\ b_{21} & -b_{22} \end{pmatrix}, \tag{5.2}$$

with $b_{ij} > 0$, $i, j = 1, 2$ positive real numbers. It is straightforward that the real part of the eigenvalues of (5.2) is strictly negative. Thus, the zeroth solution of system (5.1) is asymptotically stable uniformly with respect to the initial values. We mean that, given initial values Z_0, there exist positive constants K, $\alpha \in \mathbb{R}_+$ such that

$$\|e^{Bt} Z_0\| \leq K e^{-\alpha t} \qquad \forall Z_0;\ Z_0 \leq K. \tag{5.3}$$

Getting back to our problem, let us note

$$Y(t) = \begin{pmatrix} y_1(t) \\ y_2(t) \end{pmatrix} \qquad\qquad Z(t) = \begin{pmatrix} z_1(t) \\ z_2(t) \end{pmatrix}.$$

The study of the stability of the zeroth solution of system (3.17) is carried out by means of a comparison method. Namely, given a solution of system (3.17) we build up appropriate bounding linear systems with constant coefficient similar to (5.2). The solutions of these bounding systems are upper and lower bounds for the solution of system (3.17).

For this purpose, we use appropriate choices of b_{ij}^L and b_{ij}^M for constructing each bounding system, depending on the sign of y_1 and y_2. Without lost of generality, let us begin assuming that $y_1(t_0) = y_1^0 > 0$ and $y_2(t_0) = y_2^0 > 0$. Then, in a neighborhood of t_0, it follows that

$$\begin{gathered} -b_{11}^M y_1(t) - b_{12}^M y_2(t) \leq y_1'(t) = -b_{11}(t) y_1(t) - b_{12}(t) y_2(t) \leq -b_{11}^L y_1(t) - b_{12}^L y_2(t) \\ b_{21}^L y_1(t) - b_{22}^M y_2(t) \leq y_2'(t) = b_{21}(t) y_1(t) - b_{22}(t) y_2(t) \leq b_{21}^M y_1(t) - b_{22}^L y_2(t) \end{gathered} \tag{5.4}$$

Let us consider the following bounding systems

$$\begin{cases} Z'(t) = B_L Z(t), \\ z_1(t_0) = y_1^0, \\ z_2(t_0) = y_2^0, \end{cases} \qquad \begin{cases} Y'(t) = B(t) Y(t), \\ y_1(t_0) = y_1^0, \\ y_2(t_0) = y_2^0, \end{cases} \qquad \begin{cases} W'(t) = B_M W(t), \\ w_1(t_0) = y_1^0, \\ w_2(t_0) = y_2^0, \end{cases} \tag{5.5}$$

where $B(t)$ is that of equation (3.18) and B_L and B_M are given by

$$B_L = \begin{pmatrix} -b_{11}^M & -b_{12}^M \\ b_{21}^L & -b_{22}^M \end{pmatrix} \qquad B_M = \begin{pmatrix} -b_{11}^L & -b_{12}^L \\ b_{21}^M & -b_{22}^L \end{pmatrix} \tag{5.6}$$

the Comparison Theorem yields

$$z_1(t) \le y_1(t) \le w_1(t), \qquad z_2(t) \le y_2(t) \le w_2(t), \qquad t \ge t_0 \tag{5.7}$$

at least while $z_1(t)$, $z_2(t)$, $w_1(t)$, $w_2(t)$ are kept positive, lets say, in an interval $I_0 := [t_0,\, t^*)$, with $t^* > t_0$ (it may happen that $t^* = +\infty$).

Having in mind Remark 5.1, it follows that $Z(t)$ and $W(t)$ decrease exponentially fast, and so does $Y(t)$ in I_0. It may happen that one of the components become zero after a transient time, that is, $t^* < +\infty$. Let us assume, without lost of generality, that $y_1(t^*) = 0$ and $y_2(t^*) > 0$. We recall that $\|Y(t^*)\| < \|Y(t_0)\|$. To carry on approaching the zeroth solution, let us replace the bounding systems (5.5) by another ones from t^* on.

It is straightforward that there exists $\epsilon > 0$ such that $y_1(t) < 0$, $y_2(t) > 0$ and $\|Y(t)\| < \|Y(t_0)\|$ for all $t \in [t^*, t^* + \epsilon/2]$. Thus, let us note

$$t_1 = t^* + \epsilon/2 \qquad y_1^1 = y_1(t_1) \qquad y_2^1 = y_2(t_1).$$

Considering

$$\begin{cases} Z'(t) = B_L Z(t) \\ z_1(t_1) = y_1^1, \\ z_2(t_1) = y_2^1, \end{cases} \qquad \begin{cases} Y'(t) = B(t)Y(t) \\ y_1(t_1) = y_1^1, \\ y_2(t_1) = y_2^1, \end{cases} \qquad \begin{cases} W'(t) = B_M W(t) \\ w_1(t_1) = y_1^1, \\ w_2(t_1) = y_2^1, \end{cases} \tag{5.8}$$

where $B(t)$ is that of equation (3.18) and B_L and B_M are now given by

$$B_L = \begin{pmatrix} -b_{11}^L & -b_{12}^M \\ b_{21}^M & -b_{22}^M \end{pmatrix} \qquad B_M = \begin{pmatrix} -b_{11}^M & -b_{12}^L \\ b_{21}^L & -b_{22}^L \end{pmatrix} \tag{5.9}$$

Despite of the change in the coefficients corresponding with z_1 and w_1, the left and right hand side systems (5.8) fit in Remark 5.1. Therefore, we can repeat the previous argument, so that $Y(t)$ keeps approaching zero for $t \in [t^*, t^* + K)$ for certain $K > 0$. Remark 5.1 is general enough to hold whatever super-index M or L we use in the b_{ij} coefficient for $i, j = 1, 2$.

Summing up, previous argument is independent on the sign of $y_1(t)$ and $y_2(t)$, so that it holds whatever the sign of $y_1(t)$ and $y_2(t)$ is. On the other hand, $Y(t)$ approaches uniformly exponentially fast the zero solution because of the nature of the bounding solutions.

■