Models of Applied Population Dynamics²

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Abstract

The paper is an overview of our recent results achieved with different coauthors, concerning several research lines of applied population dynamics we initiated some years ago, and mostly published in 2010. First, based on the classical Leslie population model, a dynamic demographic model including controlled immigration is recalled, and applying the Perron-Frobenius theory of nonnegative matrices, a convergent optimal control algorithm is given, in order to address the sustainability problem of the considered pay-as-you-go pension system. Then, concerning the monitoring problem of particular population systems, observer design for certain trophic chains is presented. Furthermore, considering a fish population with a reserve area, we deal with the problem of steering the population into a desired new equilibrium, applying a timedependent fishing effort as a control function. To this end, an optimal control problem is set up, which is numerically solved using an optimal control toolbox developed for MatLab. Finally, for the analysis of the efficiency of certain agents to be applied in biological pest control, corresponding mathematical models are presented that describe the dynamics of the interaction between predator, parasitoid and pest insect populations.

1. Introduction

In the paper our results concerning the methodological development in different fields of applied population dynamics are summarized. In Section 2, we present the analysis of the demographic background of the pay-as-you-go pension system. From Angrisani et al. (2004), we recall an age-structured two-sex demographic model and the existence of an asymptotic demographic equilibrium. For the analysis of the effect of a controlled immigration, in Angrisani et al. (2010), we developed an optimal control algorithm that steers

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the population towards a demographic equilibrium, and at the same time minimizes the yearly immigration. Here we shortly summarize some of the results obtained for the Italian demographic data.

Section 3 is devoted to an illustrative example of a monitoring problem of population ecology studied in Varga et al. (2010). We shortly recall the observer design for certain trophic chains of the type *resource – producer – primary consumer*. This observer system makes it possible to effectively estimate the whole state process from the observation of one of the components of the chain.

In Section 4, we consider a problem of conservation ecology: controlling a spatially structured population back to an initial equilibrium state or to a required new equilibrium by an abiotic human intervention. The results presented here are recalled from Gámez et al. (2011), and deal with a fish population present in a free fishing area and in a reserve area, with migration between them. In order to deal with the problem of steering the population to equilibrium, an optimal control problem is set up, which is then numerically solved using an optimal control toolbox developed for MatLab.

Section 5 summarizes some recent methodological developments we achieved in application of population dynamics models to biological control of insect pests, cf. Gámez et al. (2010a). Based on density-dependent models of interacting populations, the effect of the release of the predator and parasitoid agents on the pest density is analyzed.

Finally, Section 6 relates the presented material to other results of the involved authors, also discussing some further possible extensions of the presented methods.

2. Demographic model for the pay-as you-go pension system

The sustainability of a pay-as-you-go pension system strongly depends on the underlying demographic process determining the proportion of the active subpopulation to pensioners, considered as a sustainability index. In our paper Angrisani et al. (2004), based on the classical Leslie population dynamics, a two-sex demographic model has been set up.

Let *N* be the maximal age for each sex in a human population (in our simulations *N*=110); for age groups defined on yearly basis (for i = 0, 1, ..., N-1), let $x^F(t)$ and $x^M(t)$ be the N-dimensional population vectors for the female and the male sub-populations, respectively, α_i^F the female reproduction rates (counting all newborns of both sexes, i = 15, ..., 50), ω_i^F and ω_i^M the female and male survival rates, respectively (i = 0, 1, ..., N-1), $\varphi := x_0^F(0)/x_0(0)$ the sex ratio. Then for the corresponding *N*×*N* Leslie matrices and for the dynamics of the female and male sub-populations, with the *N*-dimensional basic vector $e_1 = [1, 0, ..., 0]^T$, we have

$$L^{F} \coloneqq \begin{bmatrix} 0 & 0 & \dots & \alpha^{F_{15}} & \dots & \alpha^{F_{50}} & 0 & \dots & 0 & 0 \\ \omega_{0}^{F} & 0 & \dots & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & \omega_{1}^{F} & \dots & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ \vdots & \vdots & \dots & \vdots \\ 0 & 0 & \dots & 0 & \dots & 0 & 0 & 0 & \omega_{N-2}^{F_{2}} & 0 \end{bmatrix}, \qquad L^{M} \coloneqq \begin{bmatrix} 0 & 0 & \dots & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ \omega_{0}^{M} & 0 & \dots & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & \omega_{1}^{M} & \dots & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ \vdots & \vdots & \cdots & \vdots & \cdots & \vdots & \vdots & \vdots \\ 0 & 0 & \dots & 0 & \dots & 0 & 0 & 0 & \omega_{N-2}^{M} & 0 \end{bmatrix}$$

$$x^{F}(t+1) = L^{F}x^{F}(t), \ x^{M}(t+1) = L^{M}x^{M}(t) + \frac{(1-\varphi)}{\varphi}e_{1} \circ L^{F}x^{F}(t) \quad (t=0,1,2,\ldots),$$

where \circ denotes the Hadamard product of vectors, $a \circ b = [a_1b_1, a_2b_2, ..., a_nb_n]$. For the whole population, with state vector $x = [x^F \ x^M]^T$, we have the following dynamics:

$$x(t+1) = Ax(t)$$
 (t = 0, 1, 2, ...),

where the $2N \times 2N$ block matrix Λ is defined as

$$\Lambda := \begin{bmatrix} L^F & O \\ d & 0 \\ O & L_1^M \end{bmatrix},$$

in which d and L_1^M denote the (N-1)-dimensional row vector

$$d := \begin{bmatrix} 0 & \dots & 0 & \frac{1-\varphi}{\varphi} \alpha_{15}^F & \dots & \frac{1-\varphi}{\varphi} \alpha_{50}^F & 0 & \dots & 0 \end{bmatrix}$$

and the $(N-1) \times N$ matrix

respectively. In Angrisani (2004), with the application of the Perron-Frobenius theory of nonnegative matrices, the problem of demographic equilibrium (i.e. the equilibrium age distribution) has been considered. Although the standard condition of irreducibility of matrix Λ does not hold, we have managed to proof the existence of a strictly dominant positive eigenvalue and a corresponding

positive eigenvector. Hence we have also proved that the age distribution of the population converges to a demographic equilibrium, where the population growth is proportional, with rate equal to the dominant eigenvalue. As a consequence of the demographic dynamics to the pay-as-you-go pension system, we have obtained a necessary and sufficient condition for the existence of a financial equilibrium at the long term demographic equilibrium.

Recently, in Angrisani et al. (2010), the above dynamic model is modified to include a controlled immigration. A convergent algorithm is given which steers the population towards a demographic equilibrium, and at the same time minimizes the yearly immigration. In the framework of this model, choosing a parameter, the consequences of different decision strategies can be numerically analyzed in terms of the *inverse old-age dependency ratio*, considered as *sustainability index*. The results are also compared with the projections calculated under the hypotheses that the yearly immigration is kept at different constant values. The simulation analysis for the *different immigration scenarios* is carried out with the Italian data of 2006 provided by the Italian Institute for Statistics. *Scenario A*: prescribed constant yearly immigration. In our case, according to the Italian law in force, this figure is yearly set at 180.000. *Scenario B*: the *de facto* present yearly immigration, kept constant, set at 500.000. *Scenario C*: immigration controlled by our model.



Figure 1. Dynamics of the age distribution for Scenario C



Figure 2. Inverse old-age dependency ratio for the three scenarios



Figure 3. Total immigration per year for Scenario C

Of course, the analysis of the demography underlying the pension system is the very first step towards a complex solution also including the important socioeconomic components.

3. Observer design for trophic chains

At the beginning of this research line concerning monitoring, the study was concentrated on basic qualitative properties of population ecological models. One of them is observability which, for population systems, means that from partial observation of the system (observing only one or several indicator species), in principle, the whole state process can be recovered. Recently, for different ecosystems, the so-called *observer system* (or state estimators) have been constructed that enables us to effectively estimate the whole state process from the observation. Below, from Varga et al. (2010) we shortly recall the observer design for certain trophic chains of the type *resource – producer – primary consumer*.

The considered model describes how a resource moves through a trophic chain. A typical terrestrial trophic chain consists of the following components:

resource, the 0th trophic level (solar energy or inorganic nutrient),

which is incorporated by

a plant population, the *I*st trophic level (producer),

which transfers it to

a herbivorous animal population, the 2^{nd} trophic level (primary consumer).

According to the possible types of 0^{th} level (energy or nutrient), two types of trophic chains can be considered: *open chains* (without recycling) and *closed chains* (with recycling). At the 0^{th} trophic level, resource is the common term for energy and nutrient.

Let x_0 denote the time-varying quantity of free resource, say nutrient present in the system, x_1 and x_2 , in function of time, the biomass (or density) of the producer (species 1) and the primary consumer (species 2), respectively. Let Q be the resource supply considered constant in the model. Let $\alpha_0 x_0$ be the velocity at which a unit of biomass of species 1 consumes the resource, and assume that this consumption increases the biomass of species 1 at rate k_1 . A unit of biomass of species 2 consumes the biomass of species 1 at velocity $\alpha_1 x_1$, converting it into biomass at rate k_2 . Both the plant and the animal populations are supposed to decrease exponentially in the absence of the resource and the other species, with respective rates of decrease (Malthus parameters) m_1 and m_2 .

Finally, in a closed system the dead individuals of species 1 and 2 are recycled into nutrient at respective rates $0 < \beta_1 < 1$ and $0 < \beta_2 < 1$, while for an open system (where there is no natural recycling) $\beta_1 = 0$, $\beta_2 = 0$ holds. Then with model parameters

$$Q, \alpha_0, \alpha_1, m_1, m_2 > 0$$
. $k_1, k_2 \in [0,1[; \beta_1, \beta_2 \in [0,1[, \beta_1, \beta_2 \in [0,1], \beta_1, \beta_2 \in [0,1[, \beta_1, \beta_2 \in [0,1], \beta_1, \beta_2 \in [0,1], \beta_1, \beta_2 \in [0,1], \beta_1, \beta_1, \beta_2 \in [0,1], \beta_1, \beta_1, \beta_2 \in [0,1], \beta_1, \beta_1, \beta_2 \in [0,1], \beta_1, \beta_2 \in [0,1], \beta_$

for the trophic chain the following dynamic model can be set up:

$$\dot{x}_{0} = Q - \alpha_{0} x_{0} x_{1} + \beta_{1} m_{1} x_{1} + \beta_{2} m_{2} x_{2}$$

$$\dot{x}_{1} = x_{1} (-m_{1} + k_{1} \alpha_{0} x_{0} - \alpha_{1} x_{2})$$

$$\dot{x}_{2} = x_{2} (-m_{2} + k_{2} \alpha_{1} x_{1})$$
(3.1)

It can be shown that if the resource supply is high enough then this system has a unique equilibrium $x^* = (x_0^*, x_1^*, x_2^*) > 0$. Let us suppose that, for a monitoring of the system, the time-varying quantity of free resource (more precisely, its deviation from its equilibrium value) is observed:

$$y = x_0 - x_0^*$$
 (3.2)

In Varga et al. (2010), it has been proved that observation system (3.1)-(3.2) is locally observable which means that near the equilibrium x^* , from observed function y, the state of system (3.1) can be uniquely recovered. For the actual state estimation an auxiliary system, the so-called observer system can be constructed, the solutions z of which exponentially approaches the unknown solution x of the original system.

Example 3.1. As a numerical example, we consider the following parameter values:

$$Q := 10; \,\alpha_0 := 0.3; \,\alpha_1 := 0.1; \,\beta_1 := 0.2;$$
$$\beta_2 := 0.3; \,m_1 := 0.1; \,m_2 := 0.4; \,k_1 := 0.5; \,k_2 := 0.5$$

Now the a positive equilibrium of system (3.1) is $x^* = (4.52, 8, 5.78)$, and the observer system corresponding to (3.1)-(3.2) is

$$\dot{z}_{0} = 10 - 0.3z_{0}z_{1} + 0.2 \cdot 0.1z_{1} + 0.3 \cdot 0.4z_{2} + 10[y - (z_{0} - x_{0}^{*})]$$

$$\dot{z}_{1} = z_{1}(-0.1 + 0.5 \cdot 0.3z_{0} - 0.1z_{2})$$

$$\dot{z}_{2} = z_{2}(-0.4 + 0.5 \cdot 0.1z_{1}) + 1[y - (z_{0} - x_{0}^{*})].$$
(3.3)

If we set initial condition x(0) := (3, 7, 2) near the equilibrium $x^* = (4.52, 8, 5.78)$, and similarly, we consider another nearby initial condition, z(0) := (2.9, 7.2, 1.8) for the observer system (3.3), Figure 2 shows that the corresponding solution *z* approaches the solution *x* of the original system (3.1).



Figure 3.1. Solutions of system (3.1) and its observer (3.3)

4. Equilibrium control of a fishery model with reserve area

In addition to observation (or monitoring), control is also an important issue in conservation ecology. In particular, for a population system, in an appropriate setting, controllability implies that a disturbed ecosystem can be steered back to an equilibrium state, or to a new equilibrium by an abiotic human intervention. Recent research concerns the effective calculation of such control functions.

In Gámez et al. (2011) the following dynamic fishing effort model was considered. Let $x_1(t)$ and $x_2(t)$ be the biomass densities of the same fish population inside a free fishing area and a reserve area, respectively, at a time t. We suppose the population growth is logistic in each area, the fish subpopulation of the free area migrate into reserve area at rate m_{12} , and the inverse migration rate is m_{21} . Let E be the fishing effort applied in the free area. Then dynamics of the population system can be described by equations

$$\dot{x}_{1} = r_{1}x_{1}\left(1 - \frac{x_{1}}{K_{1}}\right) - m_{12}x_{1} + m_{21}x_{2} - qEx_{1}$$

$$\dot{x}_{2} = r_{2}x_{2}\left(1 - \frac{x_{2}}{K_{2}}\right) + m_{12}x_{1} - m_{21}x_{2}$$
(4.1)

where r_1 and r_2 are the intrinsic growth rates, K_1 and K_2 the carrying capacities in the free and reserve areas, respectively, and q is the catchability coefficient. Setting the right-hand sides of system (4.1) equal to zero, an equation for x_1 is easily obtained and the latter has a unique positive solution x_1^* if the following conditions hold:

$$\frac{r_2(r_1 - m_{12} - qE)^2}{K_2 m_{21}} < \frac{(r_2 - m_{21})r_1}{K_1},$$
(4.2)

$$(r_2 - m_{21})(r_1 - m_{12} - qE) < m_{12}m_{21}.$$
(4.3)

Now, inequality

$$\frac{r_1 x_1^*}{K_1} > r_1 - m_{12} - qE \tag{4.4}$$

implies the existence of a unique positive solution x_2^* and hence we have a unique positive equilibrium $x^* = (x_1^*, x_2^*)$. Conditions (4.2)-(4.4) will be supposed throughout this section.

Let us suppose first that the fish population is controlled by a time-dependent fishing effort of the form E+u(t), where u is defined on a fixed time interval [0,T]. Then from model (1.1) we obtain the control system

$$\dot{x}_{1} = r_{1}x_{1}\left(1 - \frac{x_{1}}{K_{1}}\right) - m_{12}x_{1} + m_{21}x_{2} - q(E + u(t))x_{1}$$

$$\dot{x}_{2} = r_{2}x_{2}\left(1 - \frac{x_{2}}{K_{2}}\right) + m_{12}x_{1} - m_{21}x_{2}.$$
(4.5)

Applying a linearization method, for control system (4.5) it can be proved that it is locally reachable from x^* in time *T*. The latter means that, using an appropriate control, the system can be steered from x^* to any point of a neighbourhood of x^* . In fact, for a given y^* from this neighbourhood, we can calculate a control function (a time-dependent fishing effort) such that for the corresponding solution x the distance between x(T) and y^* is minimal (i.e. zero by reachability). This optimal control problem can be numerically solved using an optimal control toolbox developed for MatLab in Banga et al. (2005) and Hirmajer et al. (2009). Once the system is in state y^* , with an appropriate constant fishing effort E1, this new equilibrium can be maintained, as illustrated in the following

Example 4.1. For a numerical illustration let us consider the following model:

$$\dot{x}_{1} = 0.7x_{1}\left(1 - \frac{x_{1}}{10}\right) - 0.2x_{1} + 0.1x_{2} - 0.25 \cdot 0.9x_{1}$$

$$\dot{x}_{2} = 0.5x_{2}\left(1 - \frac{x_{2}}{2.2}\right) + 0.2x_{1} - 0.1x_{2}$$
(4.6)

For this system conditions (4.2)-(4.2) are satisfied, and it has a nonnegative equilibrium $x^* = (4.85, 3.12)$, corresponding to a constant fishing effort E=0.9. Suppose that we want to steer the system in the new equilibrium $y^* = (1.86, 2.43)$ by the time moment T=5. The obtained results are shown in Figure 4.1.



Figure 4.1. Control function and solution of system (4.5) for T=5, with initial value x(0)=(4.85,3.12)

5. Biological pest control

The South American tomato pinworm, Tuta absoluta (Meyrick), from its entrance in Spain in 2006, turned out to be a pest with hard economic consequences both in greenhouse and open field tomato crops (Cabello, 2009). From that time on, a work has been going on with autochthonous parasitoid natural enemies that could be adapted to this new prey/host and would admit the development of a biological pest control program (Cabello et al., 2009a,b). Principally, two species have been studied: the egg parasitoid Trichogramma achaeae (Nagaraja & Nagarkatti) and the predator Nesidiocoris tenuis (Reuter). This study was aimed at setting up a mathematical model that would enable us to program the use of the mentioned natural enemies (already commercially available in Spain, France and Morocco), depending on the pest population dynamics in greenhouse tomato crops. The application of systems analysis techniques contributed to the better understanding of the biological control and its practical application (Gámez et al., 2000; Cabello et al., 2008; Tellez et al., 2009).



The present work has been motivated by the need to study the intra- and interguild relations between several species. These relations can play a very important role in the efficacy of the utilization of natural enemies. The objective of the present work has been to present mathematical phytophagous-predator (-parasitoid) models that would be applied in the utilization of T. absoluta in biological control.

The data used for the construction of the model have been collected in years 2008 and 2009 in experimental greenhouse, utilizing techniques of control by means of the application of Trichogramma achaeae and Nesidiocoris tenuis, as we can see in Cabello (2009). To these data the following mathematical models have been applied:

Phytophagous-parasitoid model

$$\dot{x}_1 = x_1 (m_1 - \gamma_1 x_2)$$

$$\dot{x}_2 = x_2 (-m_2 + k_{21} \gamma_1 x_1),$$

where x_1 and x_2 are the density (number/plant) of T. absoluta and T. acaeae, respectively, m_1 the growth rate of the pest, γ_1 the parasitation rate, m_2 the mortality rate and k_{21} the emergency rate of parasitoids.

Phytophagous-parasitoid-predator model

$$\begin{aligned} \dot{x}_1 &= x_1 (m_1 - \beta_1 x_1 - \gamma_1 x_2 - \alpha_1 x_3) \\ \dot{x}_2 &= x_2 (-m_2 + k_{21} \gamma_1 x_1 - \beta_2 x_2 - k_{23} \gamma_1 x_3) \\ \dot{x}_3 &= x_3 (m_3 + k_{31} \alpha_1 x_1 + k_{32} \gamma_1 x_2 - \beta_3 x_3). \end{aligned}$$

Here x_3 is the density (number/plant) of N. tenuis, β_i (i = 1, 2, 3) the coefficients of intra-specific competition, α_i the predation rate, k_{23} the predation rate of parasitized prey; m_2 the mortality rate, k_{31} the conversion rate of prey, k_{32} the conversion rate of parasitized prey and the rest of coefficients have meanings analogous to those of model a). In both cases the adjustments have been done with the software SimFit 6.1 (Bardsley, 2007) for the data of the first and second generation of the pest (T. absoluta) collected in greenhouses.

The results obtained in Gámez et al. (2010a) are the following: To the data collected on the activity of predation by N. tenuis and parasitism by T. achaeae, on pest eggs (T. absoluta) in commercial tomato crops in Spanish greenhouses, a good fit was found for model a) of the phytophogous-parasitoid interaction. The model fitting is shown in Figure 1 for the first, and in Figure 2 for the second generation of pest. We can conclude, on the one hand, that the pest responds well to the presence of the parasitoid, with quickly reducing density, according to model a). On the other hand, we got good fit of for model b), therefore, the presence of the predator does not explain the dynamic behaviour of the pest population. Consequently, in the phytophagous-parasitoid-predator system, the main agent against T. absoluta is T. achaeae, and N. tenuis plays only a complementary role.



Figure 5.1. Dynamics of population of the first generation of T. absoluta, in comerciale greenhouse conditions of tomato, in the system phytophagous (T. absoluta)-parasitoid (T. achaeae)-predator (N. tenuis)



Figure 5.2. Dynamics of population of the second generation of T. absoluta, in comercial greenhouse conditions of tomato, in the system phytophagous (T. absoluta) --parasitoid (T. achaeae)-predator (N. tenuis)

6. Discussion and outlook

As an alternative to the optimal immigration control of the demographic model presented above, sustainability criteria of different forms can also be formulated, in order to find optimal immigration strategies. The presented dynamic analysis of the demography underlying the pension system is the very first step towards a complex model also including the socio-economic component. For a more comprehensive model, not only predictions on the demographic parameters should be taken into consideration, but a dynamic description of employment, economic growth (at least in terms of possible scenarios) and the social costs of the integration of immigrants have to be included.

Concerning the observer design for population systems, we note that and approach similar to the presented one can be applied for the monitoring of general food webs and many different multispecies dynamic population models, see e.g. Cressman and Garay (2003, 2006), Cressman et al. (2004), Garay (2002). The applied methodology can also be extended to more complex models of food webs, involving the observation of certain abiotic environmental components and/or certain indicator species. Furthermore, it can also be useful for the monitoring of population systems in changing environment, where the change of certain abiotic parameters of the ecosystem is governed by an "external" dynamic system (describing e.g. an industrial pollution or climatic changes), see Gámez et al. (2008b). For an iterative method of observer design see Gámez et al. (2008a).

As for the dynamic fishing effort model with reserved area, the ongoing research is aimed at the monitoring and optimal harvesting problems. This fishery model can also be extended to general spatially structured (patchy) populations, with linear diffusion between patches. Recently, control problems for trophic chains have been considered in López et al. (2010). Both monitoring and control problems of particular structured cell populations have been studied in the context of radiotherapy in Gámez et al. (2009).

For further recent research on biological control has been published in Gámez et al. (2010b), where with an appropriate functional response, a dynamic model was given for the application of the egg-larval parasitoid Chelonus oculator (Panzer) as an agent against the pest Beet Armyworm, Spodoptera exigua (Hubner) in greenhouse crops.

We also note that while in the study recalled in Section 5, the considered models are set up in terms of total densities of the species involved, in an ongoing research reported in Sebestyén et al. (2011), a stage-structured dynamic model has been built for the description of the temperature-dependent development of a host-parasitoid system of insect populations, in order to find the optimal timing of the release of parasitoid agents to control a pest population.

Finally, in the interface between applied population dynamics and population genetics, in Sebestyén et al. (2010) a dynamic harvesting model was set up, where in a size-structured population model, an additional genetic structure was also included, and the effect of harvesting on the genetic composition of the population was studied.

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