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# Analysis of an efficient integrator for a size-structured population model with a dynamical resource

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ABSTRACT

In this paper, an efficient numerical method for the approximation of a nonlinear size-structured population model is presented. The nonlinearity of the model is given by dependency on the environment through the consumption of a dynamical resource. We analyse the properties of the numerical scheme and optimal second-order convergence is derived. We report experiments with academical tests to demonstrate numerically the predicted accuracy of the scheme. The model is applied to solve a biological problem: the dynamics of an ectothermic population (the water flea, *Daphnia magna*). We analyse its long time evolution and describe the asymptotically stable steady states, both equilibria and limit cycles.


## 1. Introduction

In nature we observe that some physiological characteristics, like age, level of satiation (of a predator), energy reserves or the body size of the individual, play an important role in its behaviour. Physiologically structured population models express the dynamics of the population in terms of the processes taking place at the basic unit (individual level) considering physiological differences. They describe the changes in the number of individuals of a population due to growth, death and reproduction and reflect the effect of the physiological state of the individuals on the population dynamics.

Unlimited population growth does not exist either. A population influences its environment and therefore its own behaviour. In addition, many biological feedback loops can only be described properly in terms of the interaction of the physiological processes within the individuals (e.g. the availability of food). Consequently, the use of nonlinear structured population models is an ideal tool to give a realistic mathematical formulation of density dependence. They allow us to take into account the effect of competition for natural resources in the structured-specific growth, mortality and fertility rates.

In this paper, we study a situation in which the vital rates are influenced by the availability of food in the environment, for which the individuals in the population compete. The dynamics of food density is determined by two processes: the regeneration of the food within the environment (which models the changes in the food density in the absence of any consumers) and the feeding by the individuals of the physiological structured population. It could be explained as a predator–prey model in which the predator is considered physiologically structured and the prey is unstructured. A similar theoretical framework could be found when we try to model the dynamics of a cellular population for a continuously stirred batch culture in a tank reactor [1]. In this case, the model includes a different integral term which takes into account how cells divide. With respect to individual growth rate, a fraction of the ingested food is channelled to maintenance and growth. The necessity of maintenance could make this quantity negative. Therefore, the animal shrinks in fact (sea-anemones, flatworms, water fleas, etc.) [2–4].

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Theoretical analysis of these kinds of problems is highly difficult. With respect to models with a nonlinear dependence on weighted populations, the analysis of existence and uniqueness was proven in [5]. Calsina et al. [6] made an in depth theoretical study in two settings: a finite and infinite size range, although it was made only in the case of the nonlinear autonomous case. It was pointed out in [4], that for an analysis of models that involves a dynamical resource we had to perform as carried out in [6]. The study of this theoretical framework appeared first in a Thieme's presentation http://math.la.asu.edu/~dieter/workshop/schedule.html. Nevertheless, a problem with only positive growth was analysed in [7]. They showed stability properties and bifurcation phenomena within a study of the renewal equation for the consumer population birth rate coupled to a delay differential equation for the resource concentration. We can find an extensive study of physiologically structured population models, with analytical studies of aspects such as existence and uniqueness, smoothness and the asymptotic behaviour of solutions in [8,2,9,10,4].

Often, models such as those discussed above cannot be solved analytically and require numerical integration to obtain an approximation to the solution. Nevertheless, standard numerical methods cannot be indiscriminately applied, because they could lead to inaccurate results and, therefore, wrong conclusions. We could introduce the following examples. We showed that the application of a non A-stable numerical method for the simulation to this problem in [11] was not suitable for the approximation of its asymptotically stable steady state. Some spurious oscillations occur if we use a wrong choice of the numerical integrator [12]. The choice of the selection procedure makes the approximation to singular asymptotically stable steady states better [13]. Also, the lack of regularity of the solution plays an essential role in using an *ad hoc* method [14].

The numerical solution to the model, due to its obvious mathematical complexity, entails a serious challenge. De Roos [3] introduced a semidiscrete method, the ''escalator boxcar train'', in terms of momenta of the original density function. However, it did not provide a direct approximation to the density function and its convergence has not yet been considered yet. In [15], we consider a direct integration of the system by means of a version of a numerical method, successfully employed in [11], to obtain this missing information. Nevertheless, it was shown that some numerical methods were not appropriate for a long-time integration. In that work, we presented a new suitable numerical method based on the modified Euler method and the mid-point quadrature rule. On the other hand, a modification of such a numerical procedure was introduced in [13] in order to approximate singular asymptotic states for these kinds of models. Details about the numerical integration of physiologically-structured population models can be found in [16] and the references therein.

On the other hand, numerical methods for the solution to these kinds of models have been successfully applied to structured models to replicate the available field and/or laboratory data for a variety of different systems: rotifers [17,18], where we showed the existence of an asymptotic stable equilibrium state and the existence of a stable periodic solution with *ad hoc* schemes due to the lack of regularity of the problem; slugs [19], in which we studied equilibrium and oscillatory solutions of a general mass structured system with a boundary delay: the numerical calculations revealed oscillations, pulse solutions and irregular dynamics; marine invertebrates [20,21], where we approximated accurately the steady states and analysed the asymptotic behaviour of the solutions to the linear model and provided original knowledge about the mechanisms that govern the stability of a nonlinear system with a dynamical larvae behaviour; forest dynamics [22,23], in which we described coexistence mechanisms in a size-structured model in terms of competitive differences at the regeneration state, etc.

Finally, when we have to face a numerical simulation in a problem, we must carry out the analysis of the following numerical properties: consistency, stability and convergence. These properties guarantee the goodness of the method to approach the solution.

In this paper, we have developed a new, more efficient second-order numerical method for the problem and performed its complete convergence analysis. We have developed numerical simulations for an academic problem to confirm numerically the convergence order. Also, we have applied it to a significant biological example: the dynamics of a *Daphnia magna* population. It has been studied numerically, but the convergence analysis for the numerical integration has not yet finished [3]. Nevertheless, an analysis of a different scheme that utilized an intermediate value to perform the numerical integration was initiated in [24]. Here, we place emphasis on the approximation to the asymptotically stable states of the model. In Section 2 we proceed to present the general model. Section 3 is devoted to introducing the numerical method employed to approximate the solution to the model. The analysis of the convergence properties is shown in Sections 4–7 and the numerical results performed complete the last section.

## 2. The model

We consider the following nonlinear size-structured population model where the population feedback on the individuals life history is given by an integro-ordinary differential equation,

$$u_t + (g(x, S(t), t)\, u)_x = -\mu(x, S(t), t)\, u, \quad 0 < x < x_M(t),\ t > 0, \tag{2.1}$$

$$g(0, S(t), t)\, u(0, t) = \int_0^{x_M(t)} \alpha(x, S(t), t)\, u(x, t)\, dx, \quad t > 0, \tag{2.2}$$

$$u(x, 0) = u_0(x), \quad 0 \le x \le x_M(0), \tag{2.3}$$

$$S'(t) = f(S(t), I(t), t), \quad t > 0, \tag{2.4}$$

$$S(0) = S^0. \tag{2.5}$$