Research paper

An age-structured population model with delayed and space-limited recruitment

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ABSTRACT

A new age-structured model for a closed population with space-limited recruitment is proposed. The problem incorporates a time delay in the settlement process representing, for a marine population of invertebrates, the pelagic larval phase previous to the sessile stage. The model possesses a nontrivial steady state which is investigated. For a deeper analysis of the stability of this equilibrium, depending on the delay, an appropriate numerical method is proposed. The nontrivial equilibrium of the numerical scheme, based on the representation of the solution along the characteristics lines, is also analyzed. For a test model associated with the dynamics of a population of barnacles, numerical experiments describing the asymptotic behavior of the solutions varying the delay are provided. In this case, the delay behaves as a destabilizing parameter of the dynamics of the model.

1. Introduction

When modeling population dynamics, age is actually one of the most natural and important parameters characterizing the population. Typically, age-structured models arise as a consequence of the balance of births and deaths across time, and they are revealed as a valuable tool for the dynamical analysis of the population. In this line, the classical Lotka–McKendrick system, though extremely simple as a model, provides fundamental insights into age-structured phenomena [1–3].

Here, we focus our attention on populations of marine invertebrates, such as barnacles, that possess sessile adults and pelagic larvae contained in a local area. The sessile individuals are adhered to a limited area but the larvae can freely move before their settlement. The basic processes taken into account in order to design a simple model describing the dynamics of adults are: larval recruitment, settled individuals growth and adults mortality. On the other hand, it is important to note that, for a population of sessile marine invertebrates, free space available for settlement is the obvious and principal limiting resource.

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A basic model for an open marine population of invertebrates with space limited recruitment, can be depicted by

$$\frac{\partial p(t,a)}{\partial t} + \frac{\partial p(t,a)}{\partial a} = -\mu(a)\,p(t,a), \qquad t > 0, \quad 0 < a < a_\dagger,$$

$$p(t,0) = k\,(A - s(t)), \qquad t > 0,$$

$$s(t) = \int_0^{a_\dagger} \beta(a)\,p(t,a)\,da, \qquad t > 0,$$

$$p(0,a) = p_0(a), \qquad 0 \le a < a_\dagger,$$

where $p(t,a)$ denotes the density of adults of age a at time t. In the balance law, describing aging and dying, $\mu(a)$ is the age-specific death rate. In the boundary condition, representing the settlement process, k is the instantaneous settling rate per unit of free space, A is the total area of available substrate and $s(t)$ is the occupied space by the individuals at time t (then, $A - s(t)$ provides the size of free space available by the larvae). In the occupied space, $\beta(a)$ is the size of the individual of age a. Last equation establishes the initial configuration given by $p_0(a)$. In the problem, $a_\dagger$ represents the maximum age of individuals. Note that this model describes an open system because the reproductive cycle is not closed: newly settled larvae can be carried from outside the region.

This is a modification of the original model by Roughgarden et al. [4], considered in [5,6], which incorporates a finite value of $a_\dagger$, a mathematically tractable assumption that is reasonable from a biological point of view. With respect to the vital functions: $\beta \in L_+^\infty(0, a_\dagger)$, and $\mu(a)$ is positive and locally integrable on $[0, a_\dagger)$, satisfying that

$$\int_0^{a_\dagger} \mu(a)\,da = +\infty. \tag{1}$$

Hypothesis (1) assures that every individual dies before the limit age because the survival probability, the proportion of newly settled larvae who can survive to age a given by

$$l(a) := \exp\left(-\int_0^a \mu(\sigma)\,d\sigma\right), \tag{2}$$

vanishes at the maximum age $a_\dagger$.

It is known that the previous system possesses a unique positive steady state, and the stability of this equilibrium has been analyzed in [4–6]. For example, an essential result is the so-called "fifty percent free space rule"(see [6]): if the proportion of free space at the steady state is greater than one half, then the steady state is globally asymptotically stable.

A more general recruitment process for this open marine population model has been considered in [7]. In that work, the steady state of the corresponding system has been analyzed, and the rich dynamics of the solutions have been revealed from a numerical point of view.

Most marine populations are thought to be well connected via long-distance dispersal of larval stages. However, the alternative process of larval retention near local populations is shown to exist and may be of great importance in the maintenance of marine population structure and management of coastal marine resources [8]. Therefore, closed models could be of interest in the description of these populations.

In order to close the reproduction cycle of the population, different alternatives to the model have been considered. In [9], a closed metapopulation, composed of many local subpopulations contributing larvae into the common larval pool, is presented. In [10], the population is divided in different life stages: sessile adults and pelagic larvae, and the model incorporates the contribution of the latter population to the recruitment process from the former. The problem involves a coupled system of differential equations describing the dynamics of the different stages. A numerical investigation of the mechanisms that govern the stability of this system has been carried out in [11].

Based on this last idea, here we propose a simple model which incorporates, into the settlement process, the space limitation for the passage of adulthood as well as the reproductive mechanism in order to close the system. Moreover, the larval stage of new individuals is observed by means of a time delay in the incorporation of newborns to the sessile population.

In Section 2 we introduce the new age-structured population model, we characterize the positive steady state of the system and investigate its stability. In Section 3 we describe a numerical method for the numerical approximation of the solution to the model, and justify the value of this scheme to provide additional information related to the dynamics of the model. In Section 4, for a test model associated with the dynamics of barnacles, we carry out an extensive numerical simulation that shows the effect of the delay in the behavior of the solution. In Section 5 we discuss the results obtained.

2. The model

We modify the basic open model described in Section 1 in order to close the reproductive cycle of the population. In addition, we introduce a time τ, $0 \le \tau < a_\dagger$, which represents a delay in the larval recruitment. This delay can be interpreted as the period of time that lasts the pelagic larval stage of the population until the sitting. For example, it is well known that barnacle larvae typically have a minimum amount of time (2 weeks or more) that they must spend in the water before they are competent to settle [4].

As in the open model, we consider a population of sessile adults, structured by age, whose density function $p(t, a)$ satisfies the balance law

$$\frac{\partial p(t, a)}{\partial t} + \frac{\partial p(t, a)}{\partial a} = -\mu(a) p(t, a), \qquad t > 0, \quad 0 < a < a_\dagger. \tag{3}$$

With respect to the boundary condition, for a closed population with settlement limited by the occupied space, we propose the new recruitment equation

$$p(t, 0) = k \left(A - s(t) \right) s(t - \tau), \qquad t > 0. \tag{4}$$

Again, the boundary condition implicates the occupied space s, but now, evaluated at two different time levels. Therefore, the model involves these size values at time levels after $-\tau$, that is:

$$s(t) = \int_0^{a_\dagger} \beta(a) p(t, a) \, da, \qquad t > -\tau, \tag{5}$$

Finally, from the time delay in the boundary condition, we require the initial configuration over the time interval $[-\tau, 0]$, that is, we start with the initial data

$$p(t, a) = p_0(t, a), \qquad -\tau \le t \le 0, \quad 0 \le a < a_\dagger. \tag{6}$$

Notice, from (4), that the incorporation of new individuals into the existing population is limited by the amount of unoccupied space available. On the other hand, the new term included in the boundary condition represents the increase in births due to the settled population, which is described by the occupied space as a weighted function of the total size of the population. However, this magnitude appears with a delay τ corresponding to the time that the larvae stay in the water from their birth till their settlement. Now, the system is closed: the trivial density produces no newborns.

Firstly, in order to avoid the difficulties arising from the singularity of the mortality rate near the maximum age, we consider a change of variable in the problem. This change was introduced for the theoretical analysis of the original model in [6], and for its numerical analysis in [12]. So, we introduce the new unknown function $q(t, a)$, related to the density function $p(t, a)$, by means of the survival probability (2) as:

$$p(t, a) = l(a) q(t, a). \tag{7}$$

Then, the problem (3)–(6) is reduced to the following simpler one for q

$$\frac{\partial q(t, a)}{\partial t} + \frac{\partial q(t, a)}{\partial a} = 0, \qquad t > 0, \quad 0 < a < a_\dagger, \tag{8}$$

$$q(t, 0) = k \left(A - s(t) \right) s(t - \tau), \qquad t > 0, \tag{9}$$

$$s(t) = \int_0^{a_\dagger} \phi(a) q(t, a) \, da, \qquad t > -\tau, \tag{10}$$

$$q(t, a) = q_0(t, a), \qquad -\tau \le t \le 0, \quad 0 \le a < a_\dagger, \tag{11}$$

where

$$\phi(a) = \beta(a) l(a), \tag{12}$$

is the expected space size occupied by the population at age a, $\phi \in L_+^\infty(0, a_\dagger)$, and satisfies $\phi(a_\dagger) = 0$. Also, we assume that the initial configuration is $q_0(t, a) = p_0(t, a)/l(a)$, for $t \in [-\tau, 0]$, in $L_+^1(0, a_\dagger)$.

Note that we can recover the solution $p(t, a)$, to the original model (3)–(6), from the solution $q(t, a)$, to the simplified problem (8)–(11), by means of (7). Hereinafter, we deal with this new version of the system.

Unlike the original model, system (8)–(10) possesses two smooth steady states: the trivial solution, and the function q^* defined by

$$q^*(a) = \frac{A k I(\phi) - 1}{k I(\phi)^2}, \qquad 0 \le a \le a_\dagger, \tag{13}$$

where

$$I(\phi) = \int_0^{a_\dagger} \phi(a) \, da. \tag{14}$$

Actually, if $AkI(\phi) = 1$, the model only possesses the trivial equilibrium. Otherwise, in order to assure the positivity of the nonzero state (13), we impose the following condition on the parameters of the model

$$A k I(\phi) > 1. \tag{15}$$

Finally, for this nontrivial equilibrium, the associated amount of occupied space is

$$s^* = \frac{A k I(\phi) - 1}{k I(\phi)}. \tag{16}$$

In order to analyze the stability of an equilibrium, we linearize the problem at the steady state. To this end, we represent the difference between a solution of (8)–(10) and the equilibrium as:

$$u(t, a) = q(t, a) - q^*(a),$$

then the linearized system associated to this perturbation of the equilibrium is

$$\frac{\partial u(t, a)}{\partial t} + \frac{\partial u(t, a)}{\partial a} = 0, \quad t > 0, \quad 0 < a < a_\dagger, \tag{17}$$

$$u(t, 0) = k\left((A - s^*)\, S(t - \tau) - s^* S(t)\right), \quad t > 0, \tag{18}$$

$$S(t) = \int_0^{a_\dagger} \phi(a)\, u(t, a)\, da, \quad t > -\tau. \tag{19}$$

Trying out an exponential solution $u(t, a) = e^{\lambda t} u(a)$ in (17)–(19), then the following characteristic equation arises

$$1 = k\left((A - s^*)\, e^{-\lambda \tau} - s^*\right) \int_0^{a_\dagger} \phi(a)\, e^{-\lambda a}\, da.$$

For q^*, the nontrivial steady state (13) with occupied space s^* defined by (16), this equation reads

$$1 = \frac{e^{-\lambda \tau} + 1 - A\, k\, I(\phi)}{I(\phi)} \int_0^{a_\dagger} \phi(a)\, e^{-\lambda a}\, da. \tag{20}$$

Therefore, if the real part of a complex root λ of the characteristic equation is nonnegative, then we obtain the instability condition

$$1 \leq \left| e^{-\lambda \tau} + 1 - A\, k\, I(\phi)\right|. \tag{21}$$

For the stability analysis of the steady state we will look for conditions about the parameters which contradict (21). To this end, we try to adapt the analysis developed in [13] for a delay age-structured model.

In the case without delay ($\tau = 0$), inequality (21) is written as

$$1 \leq |2 - A\, k\, I(\phi)|, \tag{22}$$

and then we can conclude the stability of the nontrivial steady state assuming the following restrictions of the parameters

Proposition 1. *Let us consider the system* (8)–(10) *without time delay ($\tau = 0$), and the values of the parameters satisfying* (15). *Then, the steady state* (13), *with occupied space* (16), *is locally asymptotically stable if the proportion of free space at the steady state satisfies*

$$\pi := 1 - \frac{s^*}{A} = \frac{1}{A\, k\, I(\phi)} > \frac{1}{3}. \tag{23}$$

Proof. Notice that, the parameter restrictions given by (15) and (23) lead to $1 < A\, k\, I(\phi) < 3$, which contradicts (22). Therefore, under the previous conditions, in the case with no delay we deduce that all the roots of the characteristic equation have negative real parts. $\square$

Remark 1. This result can be derived from the general analysis developed in [7], for general recruitment functions, with no delay, in open population models.

Remark 2. Note that the condition (15), about the positivity of the nontrivial steady state, is equivalent to assuring that the proportion of free space at this equilibrium is strictly less than 1.

From Proposition 1, we can also conclude that, assuming (15) and (23), there exists $\overline{\tau} > 0$, such that the steady state (13) is locally asymptotically stable for $\tau \in [0, \overline{\tau})$.

On the other hand, again from the restriction (15) necessary for the positivity of the steady state, $\lambda = 0$ is not a root of the characteristic equation (20). Then, when τ increases, the stability of q^* can only be lost if any of the characteristic roots crosses on the imaginary axis. Hence, we can look for purely imaginary roots $\lambda = \pm i\omega$, $\omega \in \mathbb{R}$. In such a case, the instability condition (21) is equivalent to

$$0 \leq (A\, k\, I(\phi) - 1)\, (A\, k\, I(\phi) - 1 - 2\cos(\omega\, \tau)). \tag{24}$$

Assuming (15), there is no choice of the parameters of the model (not even (23)) which prevents (24) for all $\omega \in \mathbb{R}$.

Accordingly, we cannot assure the stability of the nontrivial steady state for large values of the time delay. Therefore, in these situations, we investigate the stability of the equilibrium from an experimental point of view.

3. The numerical method

For the numerical integration of the model with delay we adapt the scheme proposed in [12] for the open marine population model. Following that work, we deal with problem (8)–(11) obtained after the change of variable that factors out the unbounded mortality in the balance law. We consider a numerical procedure based on the discretization of the representation of the theoretical solution along the characteristic lines (for a general review about the numerical integration of age-structured population models, see [14]). To this end, note that the solution of (8) satisfies, for each $t > 0$, and a with $0 < a < a_†$, and each $h > 0$ such that $a + h < a_†$, that

$$q(t + h, a + h) = q(t, a). \tag{25}$$

For the discretization of the problem, we introduce a constant step size for both variables (time and age), that we choose as a divisor of the time delay $\tau > 0$. Therefore, given a positive integer J^*, we denote the step size $h = \tau / J^*$. On the one hand, we introduce a uniform grid over the age interval $[0, a_†]$. Then, if J denotes the nearest positive integer strictly less than $a_†/h$, we consider the discrete ages $a_j = j h, j = 0, 1 \ldots, J$, (note that $a_J < a_†$). On the other hand, we define the discrete times $t^n = n h, n = -J^*, -J^* + 1, \ldots, 0, 1, \ldots$. At each time level n, the numerical solution is described by a $(J + 1)$-dimensional vector $\mathbf{Q}^n = [Q_0^n, Q_1^n, \ldots, Q_J^n]$, where Q_j^n represents the numerical approximation to $q(t^n, a_j)$, $j = 0, 1, \ldots, J$. The numerical method consists of the discretization of (25), (9) and (10), providing a recursive procedure that describes the numerical solution $\mathbf{Q}^{n+1}$, $n = 0, 1, \ldots$, from the previously computed approximations as follows

$$Q_{j+1}^{n+1} = Q_j^n, \qquad j = 0, 1, \ldots, J - 1, \tag{26}$$

$$Q_0^{n+1} = k \left(A - S^{n+1} \right) S^{n+1-J^*}, \tag{27}$$

$$S^{n+1} = I_h(\boldsymbol{\Phi} . \mathbf{Q}^{n+1}). \tag{28}$$

The procedure is started by means of suitable approximations to the initial configuration (11). For example, we would consider the grid restriction

$$Q_j^n = q_0(t^n, a_j), \qquad n = -J^* + 1, \ldots, -1, 0, \quad j = 0, 1, \ldots, J.$$

Then, from the boundary condition (27), we use the corresponding numerical sizes of occupied space

$$S^n = I_h(\boldsymbol{\Phi} . \mathbf{Q}^n), \qquad n = -J^* + 1, \ldots, -1, 0. \tag{29}$$

In (28) and (29), the numerical method involves the values of the expected space size function ϕ, defined in (12), at the grid points, that are represented by means of the vector $\boldsymbol{\Phi}$. Furthermore, $I_h(\mathbf{U})$ denotes a quadrature rule to approximate the integral, over the interval $[0, a_†]$, of the function whose values at the grid points $a_j, j = 0, 1, \ldots, J$, are collected by the vector $\mathbf{U} = [U_0, U_1, \ldots, U_J]$. Finally, in the numerical computation of the occupied space, the vector product denoted by a dot must be interpreted component-wise.

In this work, we consider the following open quadrature formula

$$I_h(\mathbf{U}) = h U_1 + \sum_{j=1}^{J-1} \frac{h}{2} \left(U_j + U_{j+1} \right) + (a_† - a_J) U_J. \tag{30}$$

It is based on the composite trapezoidal rule but, at the first age subinterval, we use the rectangle rule based on the right node in order to obtain an explicit method and, at the last one, the rectangle rule based on the left node that avoids the maximum age.

It is important to keep in mind that the numerical method can be adapted to the model with no delay ($\tau = 0$) by using (26)–(28): we state $J^* = 0$ and, for an arbitrary integer positive J, we define $h = a_†/(J + 1)$. Now, we start the method with $Q_j^0 = q_0(0, a_j), j = 0, 1, \ldots, J$.

In any case, regardless of the size of the delay (including $\tau = 0$), the scheme possesses two steady states: the trivial one, and the numerical counterpart of (13), $\mathbf{Q}^* = [Q_0^*, Q_1^*, \ldots, Q_J^*]$ described by

$$Q_j^* = \frac{A k I_h(\boldsymbol{\Phi}) - 1}{k I_h(\boldsymbol{\Phi})^2}, \qquad j = 0, 1, \ldots, J. \tag{31}$$

For the nontrivial equilibrium, the amount of occupied space is

$$S^* = \frac{A k I_h(\boldsymbol{\Phi}) - 1}{k I_h(\boldsymbol{\Phi})}. \tag{32}$$

As for the model, we impose

$$A k I_h(\boldsymbol{\Phi}) > 1, \tag{33}$$

which establishes that the numerical steady state (31) has positive components.

Taking into account the second-order accuracy of the composite quadrature rule (30), when it is applied to a sufficiently smooth integrand, in the following result we obtain the convergence of the equilibrium of the numerical method, as the step size goes to zero, towards the steady state of the theoretical model.

Proposition 2. *Assume that function ϕ in (12) is of class $\mathcal{C}^2([0, a_\dagger])$ and let q^* denote the steady state defined by (13). For any $h > 0$, let $\mathbf{Q}^*$ denote the steady state (31) of the numerical method.*

Then, as $h \to 0$,

$$\left| q^*(a_j) - Q_j^* \right| = \mathcal{O}(h^2), \qquad j = 0, 1, \ldots, J. \tag{34}$$

Proof. The integral $I(\phi)$ defined by (14) is positive because ϕ is a positive function on $(0, a_\dagger)$. So, from the convergence of the composite quadrature rule (30), $I_h(\boldsymbol{\Phi})$ is also positive for h sufficiently small: more precisely, fixed ε, with $0 < \varepsilon < I(\phi)$, there exists a positive h_0 such that $I_h(\boldsymbol{\Phi}) > \varepsilon$, for $0 < h \le h_0$.

Now, consider the function

$$g(\theta) = \frac{A\,k\,\theta - 1}{k\,\theta^2},$$

related with the definition of both steady states (13) and (31). Note that g is a smooth function except at $\theta = 0$. In particular, $g \in \mathcal{C}^1([\varepsilon, +\infty))$. For h, with $0 < h \le h_0$, applying the mean value theorem to this function g on the closed interval with endpoints $I_h(\boldsymbol{\Phi})$ and $I(\phi)$, we conclude that there exists θ^* in this interval such that

$$\left| q^*(a_j) - Q_j^* \right| = |g(I(\phi)) - g(I_h(\boldsymbol{\Phi}))| = \left| g'(\theta^*) \right| |I(\phi) - I_h(\boldsymbol{\Phi})|, \quad j = 0, 1, \ldots, J.$$

Then, taking into account that g' is bounded on $[\varepsilon, +\infty)$, and the second-order accuracy of the quadrature rule, we conclude (34). $\square$

Remark 3. As a consequence, condition (15) about the parameters of the model assures also the positivity of the numerical nontrivial steady state, for h sufficiently small.

If we investigate the stability of a numerical steady state, we arrive to a discrete framework similar to that achieved for the model. Denoting the difference between a numerical solution of (26)–(28) and the equilibrium as

$$U_j^n = Q_j^n - Q_j^*,$$

the linearized system associated to this perturbation of the steady state is

$$U_{j+1}^{n+1} = U_j^n, \qquad n = 0, 1, \ldots, \quad j = 0, 1, \ldots, J-1, \tag{35}$$

$$U_0^{n+1} = k\left((A - S^*)\,\Sigma^{n+1-J^*} - S^*\,\Sigma^{n+1}\right), \qquad n = 0, 1, \ldots, \tag{36}$$

$$\Sigma^{n+1} = I_h(\boldsymbol{\Phi}.\mathbf{U}^{n+1}), \qquad n = -J^*, -J^* + 1, \ldots, \tag{37}$$

If we look for a discrete solution to (35)–(37) of the form $U_j^n = \lambda^n U_j$, we obtain the characteristic equation

$$1 = k\left((A - S^*)\lambda^{-J^*} - S^*\right) I_h(\boldsymbol{\Phi}.\boldsymbol{\Lambda}),$$

where $\boldsymbol{\Lambda} = [1, \lambda^{-1}, \ldots, \lambda^{-J}]$. For $\mathbf{Q}^*$, the nontrivial steady state (31) with occupied space S^* defined by (32), this equation is equivalent to

$$1 = \frac{\lambda^{-J^*} + 1 - A\,k\,I_h(\boldsymbol{\Phi})}{I_h(\boldsymbol{\Phi})}\,I_h(\boldsymbol{\Phi}.\boldsymbol{\Lambda}). \tag{38}$$

An instability condition, similar to (21), is obtained by considering that there exists a complex root λ of (38) such that $|\lambda| \ge 1$, that is

$$1 \le \left| \lambda^{-J^*} + 1 - A\,k\,I_h(\boldsymbol{\Phi}) \right|. \tag{39}$$

The stability analysis of the nontrivial numerical steady state follows a similar analysis to that we carried out for the corresponding equilibrium of the model in the previous section.

For the numerical scheme associated to the model with no delay ($\tau = 0$), the instability condition obtained by taking $J^* = 0$ in (39) allows us to prove a discrete version of Proposition 1, in an analogous way.

Proposition 3. *Let us consider the system (26)–(28) without time delay ($\tau = 0$), and the values of the parameters satisfying (33). Then, the steady state (31), with occupied space (32), is locally asymptotically stable if the proportion of numerical free space at the steady state satisfies*

$$\Pi := 1 - \frac{S^*}{A} = \frac{1}{A\,k\,I_h(\boldsymbol{\Phi})} > \frac{1}{3}. \tag{40}$$

Remark 4. Following a reasoning similar to that we used in the proof of Proposition 2, we conclude that conditions (15) and (23), about the stability of the nontrivial steady state of the model with no delay, also establish the same behavior for the numerical equilibrium, when h is sufficiently small.

If we set a constant value of the step size h, assuming the parameter restrictions (33) and (40), we can establish the stability of the numerical equilibrium for small values of J^* and, consequently, for small values of the delay. However, when τ increases (or, equivalently, J^*), the numerical equilibrium will become unstable only if any of the roots of the characteristic equation (38) leaves the unit disk. If we test a root on the unit circle: that is, $\lambda = e^{i\omega}$, $\omega \in [0, 2\pi)$, the instability condition (39) provides a discrete version of (24). Thereby, as in the analysis performed for the equilibrium of the model, we cannot determine the local stability of the numerical steady state for large values of the time delay.

However, for the numerical method, we can resort to numerical simulation to observe the dynamics of the solutions.

4. Numerical experiments

With the following simulation we will analyze the asymptotic behavior of the numerical solutions to the model with delayed recruitment. To this end, we consider some of the vital parameters associated to a population of barnacles which were used in [4]: we take the total area of available substrate $A = 100\,\text{cm}^2$, and the maximum age of an individual $a_\dagger = 103$ weeks (that is, close to 2 years). We suppose that the area occupied by an organism increases as the power law

$$\beta(a) = M \left(\frac{a}{a_\dagger} \right)^4,$$

which represents, assuming a circular area, a growth in diameter according to the square of the age. Here, $M = 7.07\,\text{cm}^2$ is the area of a hypothetical barnacle that lives to the maximum age and corresponds to $3\,\text{cm}$ in diameter.

For the mortality rate, we consider the same function as in [7,12]

$$\mu(a) = \frac{1}{a_\dagger - a}.$$

In that case, the survival probability can be obtained from (2): that is,

$$l(a) = 1 - \frac{a}{a_\dagger}.$$

Here we use the exact values of this function at the grid points. However, note that there exist different practical numerical methods to approximate such values for more general mortality functions (see, for example, [15,16]). When using numerical approximations to the survival probability in a general linear age-structured population model with finite life-span, a converge analysis of the numerical solution to the original model before the change of variables can be found in [17]. Therefore, the expected size function is

$$\phi(a) = M \left(\frac{a}{a_\dagger} \right)^4 \left(1 - \frac{a}{a_\dagger} \right).$$

In the experiments we analyze the role of the settling rate k as a destabilizing parameter of the steady state. To this end, we take the value of k corresponding to a prescribed value of the proportion of the free space at the nontrivial steady state (13). That is, given $\pi \in (0, 1)$ we take

$$k = \frac{1}{A \pi I(\phi)} = \frac{30}{A M \pi a_\dagger}. \tag{41}$$

Remember that, from Remark 2, this choice of k assures (15).

We start the experimentation with the model with no delay ($\tau = 0$). For this case, the stability of the nontrivial steady state is established by Proposition 1, and the previous choice of the settling rate will allow us to test condition (23). To this end, we use the numerical method and perform the simulation over a period of time long enough to observe the dynamics of the solution. In the following experiments, we take the value of the step size $h = 1/7$ (representing a day): other values we have considered provide the same behavior.

With respect to the initial condition, in a similar analysis carried out in [7,12] for an open marine population model, the numerical simulation starts with the trivial initial data: the "fouling" phenomenon that represents the accumulation of organisms on an initially empty substrate. However, for the closed marine population model presented in this work, the zero function is a steady state of the model. To avoid this equilibrium, we consider a small perturbation of the fouling condition: we modify the trivial function by taking $Q_0^0 = \varepsilon$, and $Q_j^0 = 0, j = 1, \ldots, J$. This situation represents a previously empty substrate which has incorporated new larvae from the outside of the closed environment (for example, accidentally by a blow sea, or intentionally in an hypothetical barnacle farm). In the simulations we will present, we choose $\varepsilon = 0.01$.

We observe that, for the values of k corresponding to the prescribed values of π on the interval $(0.30, 1)$, the numerical solution is attracted by the corresponding steady state. In Fig. 1 we present, for some values of k (corresponding to $\pi = 0.31, 0.50, 0.70$ and 0.90 in such interval of stability), the evolution with time of the free space. As a consequence, the
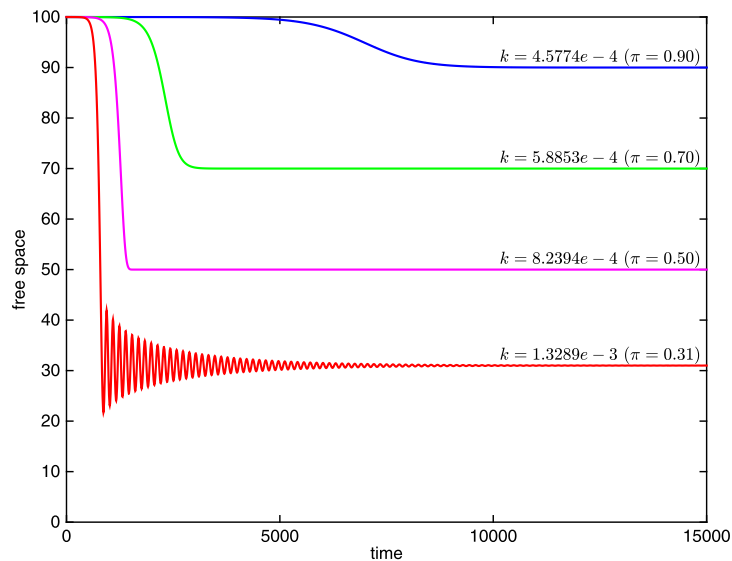
Fig. 1. Evolution of the free space for the model with no delay ($\tau = 0$), for different values of the settling rate k corresponding to a prescribed value of π, the proportion of free space at the steady state: Stable case.

numerical simulations ratify the stability condition (23). Moreover, we observe that the equilibrium is still an attractor for some values of π less or equal than $1/3$.

On the other hand, we observe a value of the settling rate ($k = 1.3732e - 3$, corresponding to $\pi = 0.30$) from which the steady state is destabilized: the numerical solution, starting from the previous initial perturbation of the fouling data, is not attracted by the equilibrium. To correctly establish this unstable situation, now we consider, as the initial condition, a small perturbation of the steady state $\mathbf{Q}^*$ described by (31): we chose $Q_0^0 = Q_0^* + \varepsilon$, and $Q_j^0 = Q_j^*, j = 1, \ldots, J$. As in the previous case, we take $\varepsilon = 0.01$.

In Fig. 2 we present the evolution with time of the free space in this unstable situation, for some representative values of k (corresponding to $\pi = 0.23, 0.24, 0.25$ and 0.26). From the numerical simulation we conclude that a change in the value of the settlement rate gives rise to a different behavior of the solution. So, for example, when $\pi \in [0.24, 0.30]$, we observe that the numerical solution is attracted to a limit cycle, a periodic solution which exhibits a different profile as the parameter k grows (see the three first pictures in Fig. 2). This periodic structure is lost for greater values of the settling rate: when $\pi \in [0.22, 0.23]$ we observe a behavior similar to chaos in the dynamics of the numerical solution (see the last picture in Fig. 2). Therefore, we note a period doubling route to chaos. Finally, when $\pi \leq 0.21$ the numerical solution blows up.

Notice that, for values of the settlement rate $k \geq 1.7165e - 3$, corresponding to $\pi = 0.24$ (third picture in Fig. 2) the simulation produces negative levels of the free space along the integration. This undesirable behavior was already noted in the original open population model [5]: such a system shows an important drawback because the population density can become negative. Therefore, we observe a similar objection for the new closed model and, then, it can only be considered useful to describe the dynamics of the populations for meaningful biological situations while the non-negativity of the solution is guaranteed.

Now we face the case with a delay ($\tau > 0$). For a given value of τ, again we vary the settlement rate taking (41) to obtain a prescribed proportion of free space at the steady state. In the experiments, for simplicity, we restrict our attention to integer values of the delay. So, in order to keep $h = 1/7$ (as in the case with no delay), we consider $J^* = 7\tau$. Again, firstly we simulate an initially empty substrate with an unexpected recruitment of external larvae. This situation is represented by the perturbation of the trivial data at $t = 0$ previously mentioned: $Q_0^0 = \varepsilon, Q_j^n = 0, j = 1, \ldots, J$; but, for $n = -J^*+1, \ldots, -1, Q_j^n = 0, j = 0, 1, \ldots, J$. We will see if the computed solution is attracted by the expected equilibrium. Otherwise, we repeat the experiment starting from a small perturbation of the numerical equilibrium described by (31): that is, for $n = -J^* + 1, \ldots, -1, Q_j^n = Q_j^*, j = 0, 1, \ldots, J$, but at $n = 0$, we modify it as we formerly established: $Q_0^0 = Q_0^* + \varepsilon, Q_j^0 = Q_j^*, j = 1, \ldots, J$. Again, we show the results obtained with $\varepsilon = 0.01$.

In Table 1, for different values of the delay, we present the stability threshold of the steady state represented by means of its limiting value that we denote $\pi_{\text{stable}}(\tau)$. Fixed τ, we vary the settlement rate k corresponding to a prescribed value of π (the proportion of free space at the steady state), and we label $\pi_{\text{stable}}(\tau)$ as the smallest value (taking two decimal places) which offers a numerical solution attracted by the steady state: a smaller π (greater k) produces instability.

On the one hand, as we expected, the stability threshold of the steady state with no delay is preserved for some positive values of τ: in this case till $\tau = 7$. On the other hand, for larger values of τ, the delay behaves as a destabilizing parameter
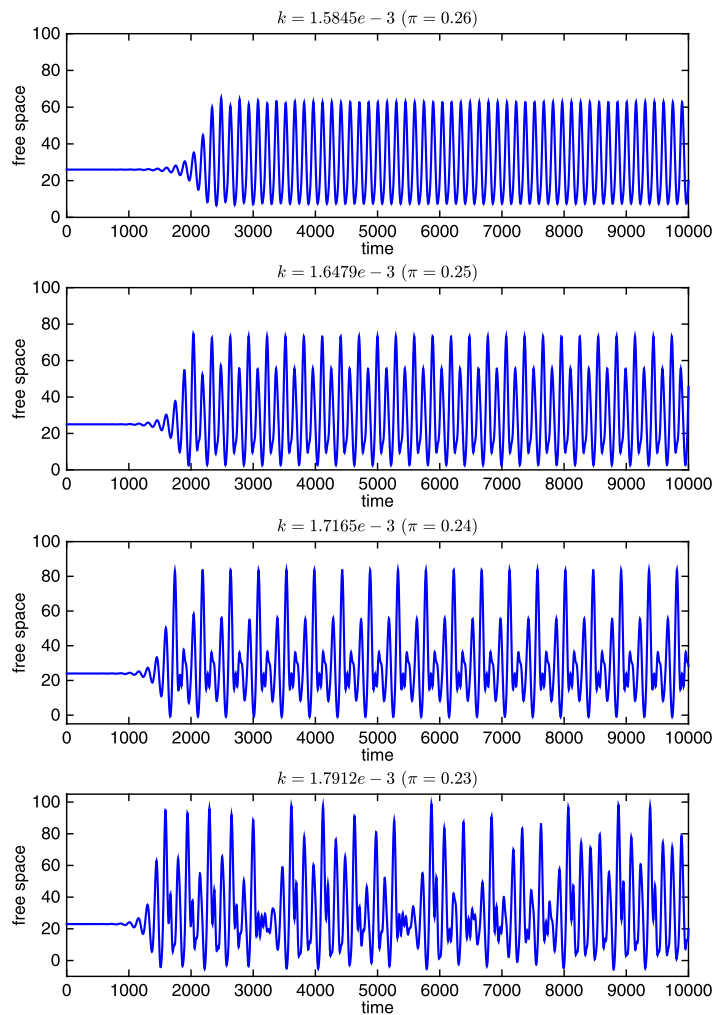
Fig. 2. Evolution of the free space for the model with no delay ($\tau = 0$), for different values of the settling rate k corresponding to a prescribed value of π, the proportion of free space at the steady state: Unstable case.

Table 1
Stability threshold of the nontrivial steady state depending on the delay.

τ	0–7	8–11	12–13	14–15	16	17–18
$\pi_{\text{stable}}(\tau)$	0.31	0.32	0.33	0.34	0.35	0.36

of the equilibrium. We observe that the interval of stability is reduced as τ increases. Notice that for $\tau = 16$, the stability condition (23), theoretically obtained for the model with no delay, is no longer fulfilled. It should be noted that, as the delay increases, this analysis becomes harder because the numerical solution exhibits very small oscillations, sustained along the simulation, which seem to be characteristic of the delay.

Finally, remember that, for a fixed value of k, the proportion of free space at the steady state is independent of τ, and the value of the delay only influences the stability of such an equilibrium: that is, in the stable case, the numerical solution is attracted by the same value, regardless of τ. However, in the unstable case, the dynamics of the numerical solution may change.

For example, returning to the value that marks the beginning of the instability interval when $\tau = 0$: $k = 1.3732e - 3$ (corresponding to $\pi = 0.30$), we deduce experimentally that the steady state is unstable regardless of the delay value $\tau \geq 0$. In the case with no delay, we observe that the solution is attracted towards a limit cycle (with a profile very similar to that presented in the first picture of Fig. 2). Considering a simulation long enough to properly observe the structure that appears, we confirm that the free space oscillates periodically (we estimate that the period is approximately $p = 148.7143$), varying between the two extreme values $f_{\min} = 21.35$, and $f_{\max} = 40.83$. When we introduce a delay, we observe a similar profile for $\tau \in [0, 17]$, but with different period and extrema. Table 2 presents, for some delays,

Table 2

Estimation, depending on the delay, of the characteristic values of the limit cycle: p, f_{min}, f_{max} represent, respectively, the period, and the minimum and the maximum values of the free space.

τ	p	f_{min}	f_{max}
0	148.7143	21.35	40.83
1	147.1429	21.60	40.38
2	145.4286	21.61	40.31
3	144.0000	21.34	40.64
4	142.2857	20.76	41.42
7	137.4286	17.27	46.45
9	133.8571	13.52	52.17
11	129.8571	8.51	59.96
13	125.2857	1.84	69.90
15	120.1429	-7.63	81.70
16	117.2857	-14.63	88.16
17	112.4286	-28.39	97.04

the characteristic values of the corresponding limit cycle. Note that, the largest values of τ in the table produce negative levels of free space, that do not make sense from a biological point of view. Lastly, for $\tau = 18$ the numerical solution blows up.

5. Concluding remarks

In this work we introduce a new model to describe the time evolution of a closed age-structure population of marine invertebrates. As in previous scenarios, the recruitment process is limited by the amount of free space available to larvae but, here, we close the reproduction process in order to adequately depict an isolated population. On the one hand, we include a term in the settlement process that accounts for new births produced exclusively by the existing population. As a consequence, the resulting system has richer dynamics than its predecessor the open population model: it is remarkable the appearance of limit cycles in the unstable case. On the other hand, a time delay compatible with the initial larval phase previous to the settlement stage is introduced.

The model possesses a unique nontrivial steady state and, for the case with no delay, its stability is established when the parameters satisfies that the proportion of free space at the steady state is greater than a third of the total available space. However, for the case with an arbitrary positive time delay we cannot establish, theoretically, an interval of stability of the steady state.

In order to deepen in the stability analysis of the nontrivial equilibrium, we propose a suitable numerical method for the approximation of the solutions to the model. Again, the stability of the corresponding numerical steady state is only established for a small, but indeterminate, value of the delay. However, numerical simulations provide a new perspective for studying long-time dynamics in any general case.

The experimental simulations that we have performed, for a test model associated with the dynamics of a population of barnacles, extends slightly the stability interval of the model with no delay. It also allows us to conclude that the stability threshold of the steady state is maintained over a certain interval of the delay, starting from zero, which we compute experimentally. Out of this range, the delay is a destabilizing parameter of the equilibrium. Finally, in the unstable case, the numerical method reveals itself as a valuable tool for the asymptotic analysis of the solutions to the model.

CRediT authorship contribution statement

Óscar Angulo: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Funding acquisition. **Juan Carlos López-Marcos:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Funding acquisition. **Miguel Ángel López-Marcos:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Funding acquisition. **Julia Martínez-Rodríguez:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Funding acquisition.

Declaration of competing interest

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

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