Persistence and Extinction in Spatial Models with Carrying Capacity Driven Diffusion and Harvesting

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Abstract

For the reaction-diffusion equation

$$\frac{\partial u(t,x)}{\partial t} = D\Delta\left(\frac{u(t,x)}{K(t,x)}\right) + r(t,x)u(t,x)g\left(K(t,x),u(t,x)\right) - E(t,x)u(t,x)$$

with the general type of growth, diffusion stipulated by the carrying capacity K and harvesting, existence, positivity, persistence, extinction and stability of solutions are investigated. In numerical simulations, the results are compared to the model with a regular diffusion.

Keywords. Diffusion, harvesting, positive periodic solution, global attractivity, rate of convergence, logistic law, Gilpin-Ayala growth, Gompertz function, maximal yield

AMS subject classification: 92D25, 35K57 (primary), 35K50, 37N25

1 Introduction

A natural way to introduce spatial movements in the models of population dynamics is to add the diffusion term in the right hand side of the equation, which in many cases leads to the uniform ideal free distribution (see, for example, [2, 27]). For models with unequally distributed resources (nonconstant carrying capacity of the environment), this may lead to the possibility of massive migration from the places with high per capita available resources to less fertile areas, which is a questionable strategy. Moreover, the fitness of the population decreases as the diffusion coefficient increases [13]. This leads to an unreasonable conclusion that the ability to disperse quicker leads to evolutionary disadvantages. There were several other approaches to describe movements in the models

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of fire or disease spread, chemotaxis and some other models, see the recent papers [1, 20, 22] and references therein; there were also attempts to correct the ideal free distribution by introducing an advection term in the direction of higher per capita available resources, so that the density of the population tends to the carrying capacity for large times if the advection to diffusion ratio is very high [3, 9]. In [8] Cantrell, Cosner and Lou considered a system of two competing species which use different diffusion strategies: one of the strategies discussed in the paper is the ideal-free dispersal strategy when the density of the species matches the carrying capacity of the resources. The authors also established some important results on persistence, extinction, and coexistence of the competing populations with similar growth laws and dispersal strategies.

???? As mentioned in [34], a null model for habitat patch selection in spatially heterogeneous environments is the ideal free distribution, which assumes individuals have complete knowledge about the environment and can freely disperse, see also [7]. Under the equilibrium conditions, this model predicts that local population growth rates are zero in all occupied patches, sink patches are unoccupied, and the fraction of the population selecting a patch is proportional to the patch's carrying capacity.

It is also believed (see, for example, [29]) that the number of grazing animals is related to the primary productivity (carrying capacity) of the environment. When considering invasive species, for example, *Solanum carolinense* from North America in Europe [15], it is assumed that without control (harvesting), it will spread over the whole continent, according to the available resources (mainly, climate-related issues were considered).

In [30], it was demonstrated that for non-homogeneous environment any type of purely diffusive behavior, characterized by symmetric migration rates, produces an unbalanced population distribution, i.e. some locations receive more individuals than can be supported by the environmental carrying capacity, while others receive less. Using an evolutionarily stable strategy approach, the authors show that an asymmetric migration mechanism, induced by the heterogeneous carrying capacity of the environment, will be selected.

Whether grazing animals population [29], or invasive weeds [15] or other species, or insects [26], or North American prairie ducks [33] are chosen, the observations indicated that the dispersal is asymmetric, directed to the areas of more available per capita resources. The environment properties can include productivity of food supply for herbivores, climate parameters, or human hosts for *Aedes aegypti* [26].

In the line of the abovementioned observations, we consider the carrying capacity driven diffusion where species diffuse not to less congested areas but in the direction of higher per capita available resources. This model was first introduced in [5], stability properties of the equation with the logistic type of growth were first studied in [23]. One important observation that should be made here is about the way we introduce a diffusion term in the equation. Usually, in the case of random dispersal of species the diffusion term takes the form $d\Delta u$, where d is the diffusion coefficient, and u is the density of the species. In this case the dimension of d is m^2/s. However, in case of carrying capacity driven diffusion presented here, the diffusion term has the form $D\Delta(u/K)$ where K is the carrying capacity of the environment and has the same dimensionality as u. Therefore, this new diffusion coefficient has dimension m^{2-n}/s where n is the dimension of space (usually, 1, 2 or 3), and should not be interpreted in the same way as d. When comparing the above mentioned models with two different types of diffusion, to equate the diffusion coefficients one should put $d = D/K$.

Along with non-homogeneous growth and spatial dispersal, harvesting can be involved as a part of the dynamics. This may correspond to predation, for example, to analyze plant production in the presence of herbivores [29], human harvesting, or weed [15] or pest control.

In this paper, we obtain the following main results.

1. For a general model with time and space variable growth law, harvesting and carrying capacity, the existence and uniqueness theorem, as well as persistence and extinction conditions are presented.

2. For time-independent growth law and carrying capacity, if the intrinsic growth exceeds the harvesting effort, there is a positive stationary solution, which under certain conditions attracts all positive solutions. For variable periodic parameters, there is a similar result for either a positive periodic solution or the zero equilibrium.

3. Numerical simulations confirm the theoretical results, while comparing the two models (with two different diffusion types) and partially exploring the feasible situation when harvesting exceeds the intrinsic growth rate in some parts of the domain and is smaller in the other parts.

Compared to the regular type of diffusion, the model with the carrying capacity driven diffusion has the following advantages:

1. For time-independent carrying capacity, the ideal free distribution coincides with the carrying capacity, independently of the diffusion coefficient.

2. In the case of the logistic growth, there is an advantage compared to the regular (random) diffusion independently of the diffusion coefficient [24].

3. If the carrying capacity is time-independent, an optimal continuous harvesting strategy can be developed [5] which to some extent leads to Maximal Yield over all possible harversting and diffusion scenarios, see also [6] and Section 7 of the present paper.

The paper is organized as follows. After the problem is stated and several particular cases are considered in Section 2, existence, permanence and extinction of solutions are investigated in Section 3. Section 4 considers the case when the growth law, the carrying capacity and the harvesting effort are time-independent. Under certain conditions, all positive solutions converge either to zero or to a positive stationary solution; in the absence of harvesting, this stationary solution coincides with the carrying capacity. In Section 5, the case of periodic parameters is studied, in particular existence of a positive periodic solution and its attractivity. Section 6 involves numerical simulations. Finally, Section 7 contains some discussion and presents open problems.

2 Statement of the Problem

We consider the following model

$$\frac{\partial u(t,x)}{\partial t} = D\Delta\left(\frac{u(t,x)}{K(t,x)}\right) + f(t,x,u(t,x)) - E(t,x)u(t,x), \;\; (t,x) \in Q_T \tag{2.1}$$

$$\frac{\partial\left(\frac{u}{K}\right)}{\partial n} = 0, \; (t,x) \in \partial Q_T \tag{2.2}$$

with the initial condition

$$u(0,x) = u_0(x), \; x \in \Omega, \tag{2.3}$$

where we denote

$$Q_T = (0,T] \times \Omega, \;\; \overline{Q}_T = [0,T] \times \overline{\Omega}, \;\; \partial Q_T = (0,T] \times \partial\Omega \text{ for any } \; T > 0.$$

Also denote

$$Q = (0,\infty) \times \Omega, \;\; \overline{Q} = [0,\infty) \times \overline{\Omega}, \;\; \partial Q = (0,\infty) \times \partial\Omega.$$

Here Ω is a domain in $\mathbb{R}^n$, typically $n = \{1,2,3\}$. Throughout the paper we assume that $K(t,x) > 0$ in $\overline{Q}$, $K \in C^{1+\alpha/2,2+\alpha}(\overline{Q}_T)$ for some $\alpha \in (0,1)$ and functions $K(t,x)$, $\frac{\partial K(t,x)}{\partial t}$ are uniformly bounded from below and from above in $\overline{Q}$; $E(t,x) \geq 0$, $E \in C(\overline{Q}_T)$, and $f(t,x,u)$ satisfies some of the following conditions:

(A1) f is uniformly Hölder continuous in $\overline{Q}_T \times J$, where J is either a suitable subinterval of $\mathbb{R}$ or a sector between lower and upper solutions. Moreover, functions f and $\partial f/\partial u$ are $C^1([0,T])$ as functions of t, Hölder continuous in $\overline{\Omega}$ in x variable, and continuous in $\mathbb{R}$ as functions of u.

(A2) $f(t,x,u) = u \cdot g(t,x,u)$, where $g(t,x,\cdot)$ is monotonically decreasing in $\mathbb{R}_+$ and $g(t,x,u) < 0$ when $u(t,x) > K(t,x)$ and $g(t,x,u) > 0$, when $0 < u(t,x) < K(t,x)$, $(t,x) \in Q_T$.

(A3) $g(t,x,\cdot) \in C^2(\mathbb{R})$.

It is easy to verify that once the intrinsic growth rate $r(t,x)$ is a positive bounded function, the following growth functions satisfy the assumptions (A1)-(A3).

1. Logistic growth was introduced in [32, 36], see also [25]

$$f(t,x,u(t,x)) = r(t,x)u(t,x)\left(1 - \frac{u(t,x)}{K(t,x)}\right) \tag{2.4}$$

2. Gilpin-Ayala growth [17]

$$f(t,x,u(t,x)) = r(t,x)u(t,x)\left(1 - \left(\frac{u(t,x)}{K(t,x)}\right)^{\theta}\right), \;\; 0 < \theta < 1 \tag{2.5}$$

3. Nicholson's blowflies type model (see [28, 19] for the delayed version of the model)

$$f(t, x, u(t, x)) = r(t, x)u(t, x)(e^{\alpha(1-u(t,x)/K(t,x))} - 1) \tag{2.6}$$

4. Food-limited growth [35]

$$f(t, x, u(t, x)) = r(t, x)u(t, x)\frac{1 - u(t, x)/K(t, x)}{1 + \beta u(t, x)/K(t, x)}, \quad \beta > 0 \tag{2.7}$$

5. Gompertz growth [18][1]

$$f(t, x, u(t, x)) = r(t, x)u(t, x) \ln\left(\frac{K(t, x)}{u(t, x)}\right). \tag{2.8}$$

Further, the change of variables

$$v(t, x) = \frac{u(t, x)}{K(t, x)}$$

in (2.1) leads to the following problem for the function $v(t, x)$

$$\begin{gathered}
\frac{\partial v}{\partial t} + \frac{v}{K}\frac{\partial K}{\partial t} = \frac{D}{K}\Delta v + v \cdot \tilde{g}(t, x, v) - Ev, \ (t, x) \in Q_T, \\
\frac{\partial v}{\partial n} = 0 \ \text{ on } \partial Q_T, \\
v(0, x) = u_0(x)/K(0, x) \ \text{ in } \Omega,
\end{gathered} \tag{2.9}$$

where $\tilde{g}(t, x, v) = g(t, x, Kv)$. Also denote

$$a(t, x) := (1/K) \cdot (\partial K/\partial t) + E \tag{2.10}$$

Then we can rewrite (2.9) as

$$\begin{gathered}
\frac{\partial v}{\partial t} - \frac{D}{K}\Delta v = v \cdot \tilde{g}(t, x, v) - av, \quad (t, x) \in Q_T \\
\frac{\partial v}{\partial n} = 0 \ \text{ on } \partial Q_T \\
v(0, x) = u_0(x)/K(0, x) \ \text{ in } \Omega
\end{gathered} \tag{2.11}$$

[1]Note, that the Gompertz growth function satisfies assumptions (A1), (A2) but not (A3) since $g_u(t, x, u) = -r(t, x)/u$ is not continuous at $u = 0$.

3 Existence and Permanence of Solutions

Definition 1. *The solution of (2.1)-(2.3) is* **permanent** *if there exist $m > 0$ and $M > 0$ such that*

$$m \le u(t,x) \le M, \quad t \ge t_0,\ x \in \Omega. \tag{3.1}$$

where $t_0 > 0$ depends only on u_0.

Theorem 1. *Let the function $f(t,x,u)$ satisfy the assumptions (A1), (A2) and let $u_0 \in C(\Omega)$, $u_0(x) \ge 0$ for $x \in \Omega$ and $u_0 \not\equiv 0$. Then for any $T > 0$ there exists a unique solution $u(t,x) \in C^{1+\alpha/2,2+\alpha}(\overline{Q}_T)$ of problem (2.1), (2.2), (2.3), and it is positive.*

Proof. We apply the method of upper and lower solutions to a problem (2.11) obtained after the substitution to demonstrate existence and positivity of a solution. It is easy to see that $\underline{v} \equiv 0$ is a lower solution.

Let us fix $T > 0$. To construct an upper solution consider a constant C such that

$$C \ge \sup_{(t,x)\in Q} \frac{u_0(x)}{K(t,x)} \ge \sup_{(t,x)\in Q_T} \frac{u_0(x)}{K(t,x)} \tag{3.2}$$

and

$$\tilde{g}(t,x,C) < 0$$

which can be found according to (A2). Note that since u_0 is bounded in $\overline{Q}_T$ and K is bounded from below, $\sup_{(t,x)\in Q}(u_0(x)/K(t,x)) < \infty$. Next, choose $\gamma \ge \sup_{(t,x)\in Q} |a(t,x)|$ and let $\overline{v}(t,x) \equiv Ce^{\gamma t}$. Then we have

$$\frac{\partial \overline{v}}{\partial t} - \frac{D}{K}\Delta \overline{v} = \gamma \overline{v} \ge \overline{v}\left(\tilde{g}(\overline{v}) - a\right), \quad \frac{\partial \overline{v}}{\partial n} = 0, \quad \overline{v} \ge v(0,x),$$

therefore $\overline{v}$ is an upper solution of (2.11).

To show positivity let us make the substitution

$$Z(t,x) = v(t,x)e^{At} = \frac{u(t,x)}{K(t,x)}\, e^{At},$$

where $A = \sup_{(t,x)\in Q_T} |\tilde{g}(t,x,\overline{v})| + \sup_{(t,x)\in Q_T} |a(t,x)|$. Then $Z(t,x)$ satisfies

$$\begin{gathered} \frac{\partial Z(t,x)}{\partial t} - \frac{D}{K(t,x)}\Delta Z(t,x) = (A + \tilde{g}(t,x) - a(t,x))Z(t,x) \ge 0 \\ \frac{\partial Z}{\partial n} = 0,\ (t,x) \in \partial Q_T, \\ Z(0,x) = v(0,x) \ge 0,\ x \in \Omega. \end{gathered} \tag{3.3}$$

By the maximum principle [31] $Z(t,x) > 0$ in $\overline{Q}_T$, and therefore $v(t,x) > 0$. We have demonstrated that there exists a unique positive solution $v(t,x)$ of problem (2.11). It follows from the properties of the function $K(t,x)$ that there exists a unique positive solution $u(t,x)$ of problem (2.1)-(2.3). □

As a consequence of Theorem 1 we readily obtain the following Theorem concerning the existence of global solutions of (2.1)-(2.3).

Theorem 2. *Let all the conditions of Theorem 1 be satisfied. Then for all $(t,x) \in Q$ there exists a unique solution of (2.1)-(2.3). Moreover, there exist $C > 0$ and $\gamma > 0$ such that*

$$0 \le u(t,x) \le CK(t,x)e^{\gamma t}, \;\; \forall\, (t,x) \in Q.$$

Theorem 3. *Let the function f satisfy the assumptions (A1)-(A2) and suppose there exists a constant $C > 0$ such that*

$$\Gamma := \sup_{(t,x)\in Q} (\tilde{g}(t,x,C) - a(t,x)) < 0 \tag{3.4}$$

Then there exists $t_0 > 0$ such that for any $t \ge t_0$ and $x \in \Omega$

$$u(t,x) \le M := 2C \sup_{(t,x)\in Q} K(t,x) \tag{3.5}$$

where $u(t,x)$ is the solution of the problem (2.1)-(2.3).

Proof. Let

$$B = \max\left\{ C, \sup_{(t,x)\in Q} \frac{u_0(x)}{K(t,x)} \right\}$$

and note that by (A2) the function $g(t,x,\cdot)$ is decreasing, so

$$\tilde{g}(t,x,\xi) - a(t,x) \le \Gamma$$

for any $\xi \ge C$, $(t,x) \in Q$. Then the function

$$\overline{v}(t) = Be^{\Gamma t}$$

is an upper solution of (2.11) as long as $\overline{v} \ge C$. Moreover, $\overline{v} \to 0$ as $t \to \infty$ since $\Gamma < 0$. Therefore, there exists $t_0 > 0$ such that the solution $v(t,x)$ of (2.11) is bounded above by $2C$ with C defined in (3.4). Since $2C$ is an upper solution of (2.11) provided that the initial condition is bounded by $2C$, it follows that the solution of (2.1)-(2.3) is bounded above by $2C \sup_{(t,x)\in Q} K(t,x)$ for any $t \ge t_0$ which completes the proof. $\square$

Theorem 4. *Let the function f satisfy the assumptions (A1)-(A2) and suppose there exists a constant $c > 0$ such that*

$$\gamma := \inf_{(t,x)\in Q} (\tilde{g}(t,x,c) - a(t,x)) > 0, \tag{3.6}$$

Then there exists $t_0 > 0$ such that for any $t \ge t_0$ and $x \in \Omega$

$$u(t,x) \ge m := \frac{c}{2} \inf_{(t,x)\in Q} K(t,x) \tag{3.7}$$

where $u(t,x)$ is the solution of the problem (2.1)-(2.3).

Proof. The proof is similar to the proof of Theorem 3. By Theorem 1, for any $0 < t < T$ the solution $u(t, x)$ of (2.1)-(2.3) is strictly positive. Next, let

$$b = \min \left\{ c, \inf_{(t,x)\in Q} \frac{u(\tau, x)}{K(t, x)} \right\}$$

where $u(\tau, x)$ is a solution of (2.1)-(2.3) at some moment $0 < \tau < T$. Note, that it follows from Theorem 1 that $u(\tau, x) > 0$. Next, by(A2) the function $g(t, x, \cdot)$ is decreasing and

$$\tilde{g}(t, x, \xi) - a(t, x) \geq \gamma$$

for any $0 < \xi \leq c$, $(t, x) \in Q$. Then the function

$$\underline{v}(t) = be^{\gamma t}$$

is an lower solution of (2.11) for any $t > \tau$ as long as $\overline{v} \leq c$, and $\underline{v} \to \infty$ as $t \to \infty$. Therefore, there exists $t_0 > \tau$ such that the solution $v(t, x)$ of (2.11) is bounded below by $c/2$ with c defined in (3.6). Since $c/2$ is an lower solution of (2.11) provided that the initial condition is bounded below by $c/2$, it follows that the solution of (2.1)-(2.3) is bounded below by $m := (c/2) \inf_{(t,x)\in Q} K(t, x)$ for any $t \geq t_0 > \tau > 0$. $\square$

Corollary 1. *Let the conditions of Theorems 3 and 4 hold. Then the solution $u(t, x)$ of problem (2.1)-(2.3) is permanent.*

Remark 1. *It is easy to check that for the growth functions (2.4), (2.5), (2.8), condition (3.4) is automatically satisfied. In the case of Gompertz growth (2.8) condition (3.6) is also automatic. Overall, for the permanence of solutions the following conditions are sufficient*

- *Logistic (2.4) and Gilpin-Ayala (2.5) growth*

$$\inf_{(t,x)\in Q} \left(1 - \frac{a}{r}\right) > 0$$

- *Nicholson's blowflies type growth (2.6)*

$$\inf_{(t,x)\in Q} \left(1 + \frac{a}{r}\right) > 0, \quad \frac{1}{\alpha} \ln \left(1 + \sup_{(t,x)\in Q} \frac{a}{r}\right) < 1$$

- *Food-limited growth (2.7)*

$$\inf_{(t,x)\in Q} \left(\frac{1}{\beta} + \frac{a}{r}\right) > 0, \quad \sup_{(t,x)\in Q} \frac{a}{r} < 1$$

4 Time-Independent Parameters

In this section we consider the case when the carrying capacity, harvesting effort, and growth function are time independent, i.e. $K = K(x)$, $E = E(x)$, $g = g(x, u)$. The problem (2.1)-(2.3) becomes

$$\frac{\partial u(t,x)}{\partial t} = D\Delta\left(\frac{u(t,x)}{K(x)}\right) + g(x,u)u(t,x) - E(x)u(t,x), \qquad (t,x) \in Q \tag{4.1}$$

$$\frac{\partial\left(\frac{u}{K}\right)}{\partial n} = 0, \qquad (t,x) \in \partial Q \tag{4.2}$$

$$u(0,x) = u_0(x), \qquad x \in \Omega. \tag{4.3}$$

4.1 Existence of a positive stationary solution, persistence and extinction

The next two theorems establish sufficient conditions for extinction and persistence of the population subject to continuous harvesting.

Theorem 5 justifies extinction in the case when harvesting exceeds production everywhere, while Theorem 6 establishes existence of an attracting positive periodic solution if the harvesting rate is less than the production rate at low densities.

Theorem 5. *Let the function $f(t, x, u)$ satisfy the assumptions (A1)-(A2) and let*

$$\sup_{\xi>0} g(x,\xi) < E(x)$$

for all $x \in \Omega$. Then for any $u_0(x)$ the solution $u(t, x)$ of problem (4.1)-(4.3) converges to zero as $t \to \infty$.

Proof. Let us follow the proof Theorem 1 and once again denote $v(t, x) = u(t, x)/K(x)$. Substituting $u(t, x) = v(t, x)K(x)$ in equations (4.1)-(4.3) and dividing the first equation by $K(x)$, we obtain

$$\begin{gathered}\frac{\partial v}{\partial t} = \frac{D}{K}\Delta v + \tilde{g}(x, v(t,x))v(t,x) - E(x)v(t,x),\ (t,x) \in Q,\\ \frac{\partial v}{\partial n} = 0 \ \text{ on } \partial Q,\\ v(0,x) = u_0(x)/K(0,x) \ \text{ in } \Omega.\end{gathered} \tag{4.4}$$

We will consider problem (4.4) and apply Proposition 3 from Appendix. Obviously, if $v(t, x) \to 0$ as $t \to \infty$ then $u(t, x) \to 0$ as well. First, we rewrite (4.4) in the form of (8.4) by applying the identity

$$\frac{D}{K(x)}\Delta v = \nabla \cdot \frac{D}{K(x)}\nabla v - \nabla\frac{D}{K(x)} \cdot \nabla v$$

Therefore, the function v satisfies (8.4) with $d(x) = D/K(x)$, $\vec{b}(x) = -\nabla(D/K(x))$, $\beta(x) = 0$, $F(x,v) = v\tilde{g}(x,v) - E(x)v$. Moreover,

$$F(x,v) \le (\sup_{\xi>0} g(x,\xi) - E(x))v := g_0(x)v$$

and, since $\vec{b} = -\nabla(D/K)$ is a gradient, all the differentiability conditions on the parameters of system (8.4) of Proposition 3 are satisfied. Thus, to apply Proposition 3 to system (4.4) we only need to show that the principal eigenvalue of the problem

$$\nabla \cdot \frac{D}{K}\nabla\psi - \nabla\frac{D}{K} \cdot \nabla\psi + g_0\psi = \sigma\psi, \text{ in } Q \tag{4.5}$$

$$\frac{\partial\psi}{\partial n} = 0, \text{ on } \partial Q \tag{4.6}$$

is negative. First, we multiply (4.5) by K and note that

$$K\nabla \cdot \frac{D}{K}\nabla\psi - K\nabla\frac{D}{K} \cdot \nabla\psi = D\Delta\psi$$

Next, since the eigenfunction ψ_1 corresponding to σ_1 can be chosen positive, we obtain upon multiplying (4.5) by K and integrating over Ω

$$\sigma_1 \int_\Omega K\psi_1 dx = \int_\Omega D\Delta\psi_1 dx + \int_\Omega g_0 K\psi_1 dx.$$

Boundary condition (4.6) implies

$$\int_\Omega D\Delta\psi_1 dx = -D\frac{\partial\psi_1}{\partial n}\bigg|_{x\in\partial\Omega} = 0$$

and therefore

$$\sigma_1 = \frac{\int_\Omega g_0 K\psi_1 dx}{\int_\Omega K\psi_1 dx}. \tag{4.7}$$

Since $g_0(x) = \sup_{\xi>0} g(x,\xi) - E(x) < 0$ by the assumption of the theorem we get $\sigma_1 < 0$, which concludes the proof. $\square$

Remark 2. *In the case when the assumption (A3) holds along with the assumptions (A1)-(A2), i.e. $g(x,\cdot)$ is continuously differentiable at zero, the supremum $\sup_{\xi>0} g(x,\xi)$ is attained and $\sup_{\xi>0} g(x,\xi) = g(x,0)$.*

Theorem 6. *Let the function $f(t,x,u)$ satisfy the (A1)-(A3) and let $E(x) < g(x,0)$ for all $x \in \Omega$. Then there exists a unique positive equilibrium solution $u^*(x)$ of (2.1), (2.2) such that for any nonnegative $u_0 \in C(\Omega)$, $u_0 \not\equiv 0$, we have $u(t,x) \to u^*(x)$ as $t \to \infty$.*

Proof. Proceeding similarly to the proof of Theorem 5 we obtain

$$\sigma_1 = \frac{\int\limits_\Omega (g(x,0) - E(x))K\psi_1 dx}{\int\limits_\Omega K\psi_1 dx}$$

which is positive if $E(x) < g(x,0)$. Moreover, by (A2) there exists M such that

$$G(x,v) := \tilde{g}(x,v) - E(x) < 0, \quad v > M$$

and the function $G(x,v)$ is decreasing in v for $v \geq 0$. Therefore, all the conditions of Proposition 4 from Appendix are satisfied and there exists a unique positive equilibrium solution. Moreover, since the steady state is unique then by Proposition 6 it is also asymptotically stable. □

Remark 3. *In the absence of harvesting ($E = 0$) the conditions of the theorem are satisfied by the assumptions (A2)-(A3) on the function g. Then, there always exists a unique positive equilibrium solution u^* of (2.1), (2.2); moreover, by assumption (A2) we can conclude that $u^* = K$.*

Next, we note that although the Gompertz growth function in (2.8) does not satisfy the assumption (A3) and therefore Theorem 6 is not applicable, it is possible to prove an even stronger result on the existence of a positive equilibrium.

Theorem 7. *Let $f(x,u)$ be defined by (2.8), where $r(x)$ and $K(x)$ are time-independent. Then there exists a unique positive equilibrium solution $u^*(x)$ of (2.1), (2.2).*

Proof. Substituting $v = u/K$ in (2.8), we get the following steady state problem corresponding to (4.4)

$$\begin{aligned} -D\Delta v &= -rKv\ln v - EKv, \qquad (t,x) \in Q, \\ \frac{\partial v}{\partial n} &= 0 \ \text{ on } \partial Q, \end{aligned} \tag{4.8}$$

Denote $F(x,v) = -rKv\ln v - EKv$. Since $\lim_{\upsilon\to 0}\ln v = -\infty$ it follows that there exists $\delta > 0$ such that $\hat{v} = \delta$ is a lower solution of (4.8). Moreover, $\tilde{v} = 1$ is obviously an upper solution. It is easy to check that the function $F(x,v)$ satisfies the assumption (A1) and therefore Propositions 1 and 2 from Appendix are applicable and we obtain the desired result. □

4.2 Stability of a positive stationary solution, rate of convergence

Next, let us present an estimation of the convergence type and rate to the positive equilibrium solution.

Theorem 8. *Let the function f satisfy the assumptions (A1), (A2) and suppose that there exists a unique positive equilibrium solution $u^*(x)$ of (4.1)-(4.2). Also suppose that $g_u(x, u^*(x))$ exists and is strictly negative for some $x \in \Omega$. Then for any nonnegative initial function $u_0 \in C(\Omega)$, $u_0 \not\equiv 0$, the solution $u(t, x)$ of (4.1)-(4.3) converges to $u^*(x)$ uniformly on $\overline{\Omega}$ as $t \to \infty$.*

Moreover, there exist positive numbers ρ and α such that for large t

$$|u(t, x) - u^*(x)| \leq \rho e^{-\alpha t} \psi(x) \tag{4.9}$$

where $\psi(x)$ is the principal eigenfunction of the problem linearized about u^*

$$\begin{gathered} \nabla \cdot \frac{D}{K} \nabla \psi + \nabla \frac{D}{K} \cdot \nabla \psi + \psi \Delta \frac{D}{K} + g(x, u^*)\psi + u^* g_u(x, u^*)\psi - E\psi = \lambda \psi, \quad x \in \Omega \\ \frac{\partial(\psi/K)}{\partial n} = 0, \quad x \in \partial\Omega \end{gathered} \tag{4.10}$$

Here, α can be taken any number such that $0 < \alpha < |\lambda_1|$, where λ_1 is the principal eigenvalue of (4.10).

Proof. Let us demonstrate that the hypotheses of Propositions 6 and 7 from Appendix are satisfied. First we note that there exists an $\varepsilon > 0$ such that $\hat{u} = \varepsilon u^*(x) > 0$ is a lower solution of the steady-state problem. Indeed,

$$0 = \varepsilon(D\Delta \frac{u^*}{K} + u^* g(x, u^*) - Eu^*) \leq \varepsilon(D\Delta \frac{u^*}{K} + u^* g(x, \varepsilon u^*) - Eu^*) = D\Delta \frac{\hat{u}}{K} + \hat{u} g(x, \hat{u}) - E\hat{u}$$

since the function $g(x, \cdot)$ is decreasing. Moreover, the function $\tilde{u} = K$ is an upper solution of the steady-state problem. Next, the function $F = g(x, u)u - Eu + \Delta(D/K)u$ is C^1 in u therefore the conditions of Proposition 6 from Appendix are satisfied. Moreover, it follows from Theorem 1 that for any $\tau > 0$ the solution $u(\tau, x)$ of problem (4.1)-(4.2) is strictly positive provided $u_0(x) \geq 0$ and $u_0 \not\equiv 0$. Therefore, for any initial function u_0 and $\tau > 0$ we can find a small enough $\varepsilon > 0$ such that $u(\tau, x) \in \langle \hat{u}, \tilde{u} \rangle$. By the assumption, the equilibrium u^* is unique in $\langle \hat{u}, \tilde{u} \rangle$, so the first statement of the theorem on the convergence to u^* follows.

Next, we will show that the principal eigenvalue of the problem corresponding to (4.1), (4.2) is negative. Consider the right-hand side of (4.1), which can be rewritten in the form

$$D\Delta \frac{u}{K} + g(x, u)u - Eu = \nabla \cdot \frac{D}{K} \nabla u + \nabla \frac{D}{K} \cdot \nabla u + u\Delta \frac{D}{K} + g(x, u)u - Eu$$

similar to the (8.4). Therefore, linearizing about the equilibrium u^*, we obtain the eigenvalue problem (4.10). Next, we note that the function u^* is positive and satisfies

$$D\Delta \frac{u^*}{K} + g(x, u^*)u^* - Eu^* = 0$$

therefore it is the principal eigenfunction of the problem

$$\begin{aligned} \nabla\cdot\frac{D}{K}\nabla\phi+\nabla\frac{D}{K}\cdot\nabla\phi+\phi\Delta\frac{D}{K}+g(x,u^*)\phi-E\phi=\mu\phi, \quad x\in\Omega \\ \frac{\partial(\phi/K)}{\partial n}=0, \quad x\in\partial\Omega \end{aligned} \tag{4.11}$$

with the principal eigenvalue zero. Moreover, by assumption we have $g_u(x,u^*)<0$ for some $x\in\Omega$ and by continuity also for some neighborhood of x, and therefore

$$g(x,u^*)+u^*g_u(x,u^*)-E<g(x,u^*)-E$$

on a subdomain of positive measure. Then it follows from Proposition 5 of Appendix that $\lambda_1<\mu_1$, where λ_1 and μ_1 are the principal eigenvalues of the problems (4.10) and (4.11) respectively. Thus, we obtain $\lambda_1<0$ and we can apply Proposition 7 from Appendix, which concludes the proof. □

Corollary 2. *Let the growth function f be as in any of (2.4)-(2.8). Then if there exists a positive equilibrium $u^*(x)$ of (4.1), (4.2) the solution $u(t,x)$ of (4.1)-(4.3) converges to this equilibrium as $t\to\infty$, and the convergence speed is estimated by (4.9).*

5 Periodic Parameters: Positive Solutions and Stability Analysis

In this section, we assume that the carrying capacity $K(t,x)$, the harvesting effort $E(t,x)$, and the growth function $f(t,x,u)$ are periodic in t with the same period T_0. We denote

$$Q=(0,\infty)\times\Omega, \quad \overline{Q}=[0,\infty)\times\overline{\Omega}, \quad \partial Q=(0,\infty)\times\partial\Omega$$

Once again we substitute $v(t,x)=u(t,x)/K(t,x)$, where $K(t,x)$ is assumed to be strictly positive, bounded, Hölder continuous in x, periodic and at least $C^1(\mathbb{R}_+)$ in t, and consider problem (2.11) for the function $v(t,x)$.

Theorem 9. *Suppose there exists a constant $C>1$ such that*

$$\tilde{g}(t,x,C)\le a(t,x), \ \forall\,(t,x)\in Q. \tag{5.1}$$

Further, suppose there exists c, $0<c<C$ such that

$$\tilde{g}(t,x,c)\ge a(t,x) \ \ \forall\,(t,x)\in Q \tag{5.2}$$

$$\tilde{g}(t,x,c)-c\min_{\xi\in[c,C]}|\tilde{g}_v(t,x,\xi)|\le\frac{a(t,x)}{2}+\frac{E}{2} \quad \forall\,(t,x)\in Q \tag{5.3}$$

where $a(t,x)$ is as in (2.10), and denote $\hat{v}=c$, $\tilde{v}=C$.

Then, there exists a unique periodic solution $v^*(t,x)$ of (2.11) in the interval $\langle \hat{v}, \tilde{v}\rangle$. Moreover, for any initial function $v_0(x)$ from this interval the corresponding solution of (2.11) satisfies

$$v(t,x) \to v^*(t,x) \text{ as } t \to \infty \text{ for } x \in \overline{\Omega}.$$

Proof. It is easy to check that $\hat{v}$ and $\tilde{v}$ are constant lower and upper solutions of (2.11) with the initial functions $v(0,x) = \hat{v}$ and $\tilde{v}$, respectively. Then, according to Proposition 8 from Appendix, there exists a pair of positive T_0-periodic solutions $\underline{v}$ and $\overline{v}$ satisfying

$$\hat{v} \le \underline{v}(t,x) \le \overline{v}(t,x) \le \tilde{v}, \quad (t,x) \in Q,$$

$$\frac{\partial \underline{v}}{\partial t} - \frac{D}{K}\Delta \underline{v} = \underline{v}(\tilde{g}(t,x,\underline{v}) - a(t,x)), \quad (t,x) \in Q, \tag{5.4}$$

$$\frac{\partial \overline{v}}{\partial t} - \frac{D}{K}\Delta \overline{v} = \overline{v}(\tilde{g}(t,x,\overline{v}) - a(t,x)), \quad (t,x) \in Q, \tag{5.5}$$

$$\frac{\partial \underline{v}}{\partial n} = \frac{\partial \overline{v}}{\partial n} = 0, \quad (t,x) \in \partial Q.$$

Now we will show that $\underline{v} \equiv \overline{v}$ if condition (5.3) holds. Denote $w := (\overline{v} - \underline{v})\sqrt{K}$, we subtract (5.4) from (5.5) and multiply the result by $w\sqrt{K}$ (further we will omit the dependency on t, x)

$$w\frac{\partial}{\partial t}w = D\frac{w}{\sqrt{K}}\Delta\frac{w}{\sqrt{K}} - w^2\left(\frac{a}{2} + \frac{E}{2}\right) + w\sqrt{K}(\overline{v}\tilde{g}(\overline{v}) - \underline{v}\tilde{g}(\underline{v})) \tag{5.6}$$

Due to the periodicity of K, $\overline{v}$ and $\underline{v}$, the function w is also T_0-periodic, therefore

$$\int_0^{T_0}\int_\Omega w\frac{\partial}{\partial t}w dx\, dt = \int_\Omega\int_0^{T_0}\frac{1}{2}\frac{\partial w^2}{\partial t}\,dt\,dx = \int_\Omega \left.\frac{w^2}{2}\right|_0^{T_0} dx = 0$$

Hence, integrating (5.6) we obtain

$$0 = -\int_0^{T_0}\int_\Omega D\left|\nabla\frac{w}{\sqrt{K}}\right|^2 dx\,dt + \int_0^{T_0}\int_\Omega \left[w\sqrt{K}(\overline{v}\tilde{g}(\overline{v}) - \underline{v}\tilde{g}(\underline{v})) - w^2\left(\frac{a+E}{2}\right)\right] dx\,dt$$

Next, we apply the Intermediate Value Theorem and obtain

$$\overline{v}\tilde{g}(\overline{v}) - \underline{v}\tilde{g}(\underline{v}) = (\overline{v} - \underline{v})\tilde{g}(\overline{v}) + \underline{v}(\tilde{g}(\overline{v}) - \tilde{g}(\underline{v})) = \frac{w}{\sqrt{K}}(\tilde{g}(\overline{v}) + \underline{v}\tilde{g}_v(\xi))$$

for some $\xi \in \langle \underline{v}, \overline{v}\rangle$. Therefore,

$$0 = -\int_0^{T_0}\int_\Omega D\left|\nabla\frac{w}{\sqrt{K}}\right|^2 dx\,dt + \int_0^{T_0}\int_\Omega w^2\left[\tilde{g}(\overline{v}) - \frac{a+E}{2} + \underline{v}\tilde{g}_v(\xi)\right] dx\,dt \le 0$$

where the last inequality is valid since both terms are negative according to the condition (5.3) and assumption (A2). Thus $\overline{v} - \underline{v} = 0$, and we obtain a unique periodic solution $v^* \equiv \overline{v} = \underline{v}$ of (2.11) in the interval $\langle \hat{v}, \tilde{v} \rangle$. Moreover, according to Proposition 8 from Appendix, for any initial function $v_0(x) \in \langle \hat{v}, \tilde{v} \rangle$ the corresponding solution of (2.11) satisfies $v(t,x) \to v^*(t,x)$ as $t \to \infty$ for $x \in \overline{\Omega}$. $\square$

Remark 4. *For the growth functions as in (2.4)-(2.8), the conditions (5.1)-(5.2) are the same as in Remark 1. To satisfy (5.3) as well, we have to impose additional restrictions.*

- *Logistic growth*

$$2 \sup_{(t,x)\in Q} \frac{a}{r} - \inf_{(t,x)\in Q} \frac{a+E}{2r} < 1$$

- *Gilpin-Ayala growth*

$$\sup_{(t,x)\in Q} \frac{a}{r} \left(1 - \inf_{(t,x)\in Q} \frac{a}{r}\right)^{1/\theta - 1} - \left(1 - \sup_{(t,x)\in Q} \frac{a}{r}\right)^{1/\theta} < \inf_{(t,x)\in Q} \frac{a+E}{2r}$$

- *Nicholson's blowflies type growth*

$$\sup_{(t,x)\in Q} \frac{a}{r} - \left(\alpha - \ln\left(1 + \sup_{(t,x)\in Q} \frac{a}{r}\right)\right)\left(1 + \inf_{(t,x)\in Q} \frac{a}{r}\right) < \inf_{(t,x)\in Q} \frac{a+E}{2r}$$

- *Food-limited growth*

$$\sup_{(t,x)\in Q} \frac{a}{r} - \frac{(1 - \sup_{(t,x)\in Q}(a/r))(1 + \beta \inf_{(t,x)\in Q}(a/r))^2}{(1+\beta)(1 + \beta \sup_{(t,x)\in Q}(a/r))} < \inf_{(t,x)\in Q} \frac{a+E}{2r}$$

- *Gompertz growth*

$$\sup_{(t,x)\in Q} \frac{a}{r} - \exp\left(- \sup_{(t,x)\in Q} \frac{a}{r} + \inf_{(t,x)\in Q} \frac{a}{r}\right) < \inf_{(t,x)\in Q} \frac{a+E}{2r}$$

The following result gives sufficient extinction conditions in the case of periodic parameters.

Theorem 10. *Let the growth function f satisfy the assumptions (A1)-(A2) and*

$$\sup_{\xi > 0} \tilde{g}(t,x,\xi) - a(t,x) \le -\delta, \quad \forall\, (t,x) \in Q \tag{5.7}$$

for some $\delta > 0$, where $a(t,x)$ is defined in (2.10), $\tilde{g}(t,x,\xi) = g(t,x,K\xi)$. Then, for any nonnegative $u_0(x) \in C(\Omega)$, $u_0(x) \not\equiv 0$, the solution $u(t,x)$ of problem (2.1)-(2.3) converges to zero as $t \to \infty$.

Proof. Consider problem (2.11), and let $\overline{v} = Ce^{-\alpha t}$ for some positive C, where α is to be determined later. Then we have

$$\frac{\partial \overline{v}}{\partial t} = -\alpha \overline{v}$$

and by (5.7)

$$\overline{v}(\tilde{g}(t,x,\overline{v}) - a(t,x)) \leq -\delta \overline{v}$$

Therefore, taking $C = \sup_{(t,x)\in Q}(u_0/K)$ and $\alpha \leq \delta$, we obtain that $\overline{v}$ is an upper solution of (2.11). Since $\overline{v} \to 0$ as $t \to \infty$, we have $v(t,x) \to 0$ where $v(t,x)$ is a solution of (2.11). The function $K(t,x)$ is bounded from below and above by assumption, and therefore $u(t,x) \to 0$ as $t \to \infty$, where $u(t,x)$ is a solution of (2.1)-(2.3). $\square$

Remark 5. *It is easy to see that for the growth functions (2.4)-(2.8) condition (5.7) is satisfied if the following inequalities hold*

- *Logistic, Gilpin-Ayala or food-limited growth*

$$\sup_{(t,x)\in Q} r(t,x) < \inf_{(t,x)\in Q} \left(\frac{1}{K}\frac{\partial K}{\partial t} + E \right)$$

- *Nicholson's blowflies type growth*

$$\sup_{(t,x)\in Q} r(t,x)(e^{\alpha} - 1) < \inf_{(t,x)\in Q} \left(\frac{1}{K}\frac{\partial K}{\partial t} + E \right)$$

- *Gompertz growth*
  In the case of the Gompertz growth law, the condition (5.7) is never satisfied which agrees with Remark 4 that there is always a minimal positive periodic solution.

6 Numerical Examples

In this section, we will consider numerical simulations of (2.1) with the Gilpin-Ayala growth and also compare solutions of (2.1) with a carrying capacity driven diffusion which is

$$\begin{aligned}
&\frac{\partial u(t,x)}{\partial t} = D\Delta\left(\frac{u(t,x)}{K(t,x)}\right) + r(t,x)u(t,x)\left(1 - \left(\frac{u(t,x)}{K(t,x)}\right)^{\theta}\right) - E(t,x)u(t,x), \\
&\hspace{20em} (t,x) \in Q_T \\
&\frac{\partial\left(\frac{u}{K}\right)}{\partial n} = 0, \ (t,x) \in \partial Q_T \\
&u(0,x) = u_0(x), \ x \in \Omega
\end{aligned} \tag{CD}$$

and the model with a regular (random) diffusion

$$\begin{aligned}
\frac{\partial u(t,x)}{\partial t} &= \nabla\cdot\frac{D}{K(x)}\nabla u(t,x) + r(t,x)u(t,x)\left(1-\left(\frac{u(t,x)}{K(t,x)}\right)^{\theta}\right) - E(t,x)u(t,x),\\
&\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad (t,x)\in Q_T\\
\frac{\partial u}{\partial n} &= 0,\ (t,x)\in\partial Q_T \qquad\qquad \text{(RD)}\\
u(0,x) &= u_0(x),\ x\in\Omega
\end{aligned}$$

where the diffusion coefficient is chosen to be $D/K(x)$ to match the diffusion coefficient in the model with a carrying capacity driven diffusion (CD). In all the simulations we assumed $\theta = 0.5$.

First, let us present a simple analytic example for the logistic growth illustrating that, generally, stationary solutions for equations with a regular diffusion can be strictly less than the carrying capacity of the environment.

Example 1. *Consider (RD) with time-independent parameters, $\theta = 1$, $E(x) = 0$, and $D = 1$. Let $K(x) = \cos(x) + 2$, $r(x) = \dfrac{2(2\cos(x)+1)}{(\cos(x)+2)^3}$. It is easy to check that the stationary solution of (CD) is*

$$u^*(x) = \frac{\cos(x)+2}{2} = \frac{K(x)}{2} < K(x)$$

The next example illustrates the application of Theorem 9 in the case of the Gilpin-Ayala growth function.

Example 2. *Let $\Omega = (0,1)$, $f(t,x,u) = ru(1-(u/K)^{0.5})$ and consider the problem (2.1)-(2.2) (also (CD)) with 2π-periodic in t functions*

$$K(t,x) = (2+\sin t)k(x), \quad r(t,x) = \frac{3(2+\cos t)}{2+\sin t}, \quad E(t,x) = \frac{2}{2+\sin t}$$

where $k(x)\in C^{2+\alpha}(\Omega)$, $k(x) > 0$ in $\overline{\Omega}$. Let $c = 4/9$, $C = 4$. We observe that condition (5.1) is satisfied since

$$\tilde{g}(t,x,C) = -\frac{3(2+\cos t)}{2+\sin t} < \frac{2+\cos t}{2+\sin t} = a(t,x)$$

Moreover, for $k(x) = \cos(\pi x) + 1.1$, $K(t,x) = (2+\sin t)(\cos(\pi x)+1.1)$ we have

$$a(t,x) = \frac{1}{K}\frac{\partial K}{\partial t} + E = \frac{2+\cos t}{2+\sin t} = r(t,x)(1-c^{1/2})$$

so (5.2) holds. Finally,

$$r(t,x)(1-c^{1/2}) = \frac{2+\cos t}{2+\sin t} \le \frac{8/3+(5/6)\cos t}{2+\sin t} = \frac{1}{2K}\frac{\partial K}{\partial t} + E + \frac{(1/2)rc}{C^{1/2}}$$

which confirms (5.3). Therefore, there exists a unique attracting periodic solution in the functional interval $\langle 4/9K(t,x), 4K(t,x)\rangle$. *Figure 1 illustrates convergence of several positive solutions to the unique periodic solution which is in this interval (in fact, quite close to the lower solution).*

Figure 1: The average over $\Omega = [0,1]$ of the solutions of (CD) with $K(t,x) = (2 + \sin t)(\cos(\pi x) + 1.1)$, $r(t,x) = \frac{3(2+\cos t)}{2+\sin t}$, $E(t,x) = 2/(2+\sin t)$, $D = 0.1$ and various initial functions. We observe that all solutions converge to the positive periodic solution (left), and the average of this solution is in the prescribed interval $[4/9K_{ave}, 4K_{ave}]$ (right), where K_{ave} is the average carrying capacity over space.

Next, let us compare model (RD) with the regular diffusion and equation (CD) with a carrying capacity driven diffusion. Figure 2 involves comparison of (CD) and (RD) for $t = 50$ *and of average solutions over space for* $t \in [0, 30]$.

Figure 2: Comparison of periodic solutions of the Gilpin-Ayala equation with the regular and a carrying capacity driven diffusion for $K = (2+\sin t)(\cos(\pi x)+1.1)$, $r(t) = 3(2+\cos t)/(2+\sin t)$, $E(t,x) = \frac{2}{2+\sin t}$, $D = 0.1$ at time $t = 50$ (left) and the average values over space at different times. We observe slightly higher average solutions of (CD) compared to the model with a regular diffusion in (RD).

Continuing the application of Theorem 9, we notice that for the particular case $K = (2+\sin t)(\cos(\pi x)+1.1)$ *(see Fig. 1, right) the theoretical lower solution of* $4/9K$ *was very close to the periodic solution, see a more detailed figure (Fig. 3) for the case* $K = (3+0.5\sin t)(\cos(\pi x)+1.1)$.

Example 3. *Consider a similar example without harvesting (*$E = 0$*), with* $r(t) = 3(2+\cos t)/(2+\sin t)$, $K = \cos(\pi x)+1.1$ *(time-independent),* $D = 0.1$, $\theta = 0.5$. *In Fig. 4, left, we observe that solutions of (CD) tend to the carrying capacity, while solutions of (RD) oscillate (below the average carrying capacity number). Also, in this case the average values of (RD) over space decrease with the growth of* D *and become less oscillatory in time (Fig. 4, right). In the case of the carrying capacity driven diffusion, the average values of solutions do not depend on* D.

Figure 3: The solutions of (CD),(RD) and the lower solution of (CD) for $K(t,x) = (3 + 0.5\sin t)(\cos(\pi x)+1.1)$, $r(t) = 3(2+\cos t)/(2+\sin t)$, $E = 2/(2+\sin t)$ and $t = 50$, $D = 0.1$.

Figure 4: For $r(t) = 3(2+\cos t)/(2+\sin t)$, $E = 0$ and $K(x) = \cos(\pi x) + 1.1$, the average (over space) limit solution of the Gilpin-Ayala equation with $D = 0.1$ and $\theta = 0.5$ coincides with the carrying capacity while the solution of the same equation with a regular diffusion is less (left). Moreover, the average solution of (RD) decays with the growth of D.

Example 4. *Consider the case when the parameters are time-independent, the higher intrinsic growth rate r corresponds to the higher K (which is reasonable), and harvesting is less than the natural growth rate in some areas and greater in the others. Here $r(x) = \exp(-20(x-0.5)^2)+1$, $K(x) = \exp(-10(x-0.5)^2)$, $E = 1.2$, $D = 0.1$, $\theta = 0.5$, the graphs describe evolutions of the average over $[0,1]$ solutions in time and also a distribution for t large (at $t = 200$). We observe persistence with a higher level limit solution for the carrying* *capacity driven diffusion.*

Figure 5: The averages over time (left) and the spatial profiles at $t = 200$ (right) for two different types of diffusion, where $r(x) = \exp(-20(x-0.5)^2) + 1$ is smaller than $E = 1.2$ for x close enough to the boundaries and $r > E$ in the centre of the domain. Here $K(x) = \exp(-10(x-0.5)^2)$, $D = 0.1$, $\theta = 0.5$.

Example 5. *Consider the Gilpin-Ayala model without harvesting ($E = 0$) and periodic $r(t) = 3(2+\cos t)/(2+\sin t)$, $K(t,x) = (1.1+\sin t)(\cos(\pi x)+1.1)$, $D = 0.1$ and $\theta = 0.5$. Let us compare averages over space for different stages of the cycle. For a positive periodic solution of an ordinary differential logistic equation with periodic parameters, the cycle average is less than the average of the carrying capacity, for discrete models of population dynamics this effect was studied in detail for various models, see [11, 12, 21, 14, 16] and references therein.*

In this case, the numerical simulations confirm the hypothesis that the cycle average is less than the average of the carrying capacity for partial differential equation (2.1) *without harvesting. Here the average of the carrying capacity over the time period is the top curve, a smaller delayed curve corresponds to the carrying capacity driven diffusion, and even smaller averages are for a regular diffusion (Fig. 6, left). Comparing the average values for a solution of (RD) with a regular diffusion (Fig. 6, right), we notice that the average values decrease with the growth of the diffusion coefficient D. This is coherent with the conclusion of [13] that higher diffusion coefficients in (RD) lead to evolutional disadvantage and less fitness of a population. For the carrying capacity driven diffusion, the average values of the periodic solutions of (CD) do not depend on the value of D, as numerical runs demonstrate.*

Figure 6: The left graph presents the average solutions over space of the carrying capacity and periodic solutions for (CD) and (RD), with $r(t) = 3(2 + \cos t)/(2 + \sin t)$, $K(t, x) = (1.1+\sin t)(\cos(\pi x)+1.1)$, $D = 0.1$. The line at $K \approx 1.2$ corresponds to the average of the carrying capacity both in time and space. The right graph compares the average solutions of (RD) with the same r and K, where $D = 0.1, 1, 10$.

7 Discussion and Open Problems

In the present paper, sufficient conditions for persistence and extinction, existence of a positive periodic solution and stability are obtained. Rates of convergence are analyzed in the case of time-independent parameters.

So far we have not discussed the optimal harvesting and maximal yield. However, similarly to optimal harvesting for the logistic, Gilpin-Ayala and Gompertz models in [5], the following result can be obtained.

Theorem 11. *Let the maximum of the function $f(t, x, u(t, x)) = ug(t, u(t, x))$ be attained at $u_{\max}(t, x)$ for each (t, x), where the function $u_{\max}$ satisfies*

$$\frac{\partial\left(\frac{u_{\max}}{K}\right)}{\partial n} = 0, \ (t, x) \in \partial Q_T, \tag{7.1}$$

and the functions $K(\cdot, x)$ and $g(\cdot, u)$ be T-periodic. If

$$D\Delta\left(\frac{u_{\max}(t, x)}{K(t, x)}\right) + u_{\max}(t, x)g(t, u_{\max}(t, x)) - \frac{\partial u_{\max}(t, x)}{\partial t} \geq 0 \tag{7.2}$$

for any t, x then the effort

$$E(t, x) = \left[D\Delta\left(\frac{u_{\max}}{K(t, x)}\right) + u_{\max}(t, x)g(t, u_{\max}(t, x)) - \frac{\partial u_{\max}(t, x)}{\partial t}\right] / u_{\max}(t, x) \tag{7.3}$$

provides the maximal yield over the time period T

$$MY = \int_0^T \int_\Omega u_{\max}(t,x) g(t, u_{\max}(t,x)) \; dx \; dt. \tag{7.4}$$

Proof. Let $u_{\max}(t,x)$ be the maximum of $f(t,x,u) = ug(t,u)$. First, let us note that $u_{\max}(t,x)$ is a solution of (2.1),(2.2),(2.3), with the initial condition $u_0(x) = u_{\max}(0,x)$, since it satisfies (7.1) by the assumption, it is T-periodic due to periodicity of $g(\cdot, u)$, so $\int_0^T \frac{\partial u_{\max}(t,x)}{\partial t} \; dt = 0$ for any x, and

$$\begin{aligned}
& \frac{\partial u_{\max}(t,x)}{\partial t} - D\Delta\left(\frac{u_{\max}(t,x)}{K(t,x)}\right) - u_{\max}(t,x) g(t,x,u_{\max}(t,x)) + E(t,x) u_{\max}(t,x) \\
= \; & \frac{\partial u_{\max}(t,x)}{\partial t} - D\Delta\left(\frac{u_{\max}(t,x)}{K(t,x)}\right) - u_{\max}(t,x) g(t,x,u_{\max}(t,x)) \\
& + D\Delta\left(\frac{u_{\max}}{K(t,x)}\right) + u_{\max}(t,x) g(t, u_{\max}(t,x)) - \frac{\partial u_{\max}(t,x)}{\partial t} = 0
\end{aligned}$$

for any (t,x).

Next, let $u(t,x)$ be any other solution of (2.1),(2.2),(2.3). Then, $f(t,x,u(t,x)) \leq f(t,x,u_{\max}(t,x))$, and thus the yield for $u = u_{\max}$ and E defined in (7.3)

$$\begin{aligned}
Yield &= \int_0^T \int_\Omega E(t, u_{\max}(t,x)) u_{\max}(t,x) \\
&= \int_0^T \int_\Omega \left[D\Delta\left(\frac{u_{\max}(t,x)}{K(t,x)}\right) + r(t,x) u_{\max}(t,x) g(t, u_{\max}(t,x)) \right] \; dx \; dt \\
&= \int_0^T \int_\Omega r(t,x) u_{\max}(t,x) g(t, u_{\max}(t,x)) \; dx \; dt \\
&\geq \int_0^T \int_\Omega r(t,x) u(t,x) g(t, u(t,x)) \; dx \; dt \\
&= \int_0^T \int_\Omega \left[D\Delta\left(\frac{u(t,x)}{K(t,x)}\right) + r(t,x) u(t,x) g(t, u(t,x)) \right] \; dx \; dt \\
&= \int_0^T \int_\Omega E(t, u(t,x)) u(t,x)
\end{aligned}$$

is not less than the yield for any other solution of (2.1),(2.2),(2.3), which concludes the proof. □

Condition (7.1) is satisfied, for example, if u_{max} is proportional to K (at least close to the boundary of the domain). The positivity assumption included in (7.1) is more restrictive; however, the problem of sustainable harvesting when the rapid change in $u_{\max}$ (which is usually connected to fast variations in K) and the growth rates are not high enough to catch up with quickly improving enviromental conditions, are well known in population ecology [37].

Corollary 3. *If condition (7.2) holds, then the maximum yield is attained at*

$$u_{\max} = \frac{K(t,x)}{2}, \; u_{\max} = \frac{K(t,x)}{(\theta+1)^{1/\theta}}, \; u_{\max} = K(t,x)\frac{-1+\sqrt{1+\beta}}{\beta}, \; u_{\max} = \frac{K(t,x)}{e}$$

for logistic (2.4), Gilpin-Ayala (2.5), food-limited (2.7) and Gompertz (2.8) models, respectively. For (2.6), the solution where the maximum yield is obtained does not have an immediate analytical expression, it can be computed after substituting $u_{\max}$ *into (7.4), with the appropriate function* g*.*

Finally, let us outline some open problems and topics for research and discussion.

1. In the present paper, the following two cases were considered: the harvesting effort exceeds the intrinsic growth rate everywhere (then, extinction is inevitable) and is less at every point in space and time (then, all solutions persist). Explore the case where, similar to Example 4, harvesting is greater at some points than the growth function while is smaller at the others, and obtain sufficient conditions of extinction and persistence. Among others, consider the situation when harvesting is limited to a certain area, while other parts of the domain are not harvested.

2. Consider (2.1) with the Dirichlet and the Robin boundary conditions. In this case, we can define permanence in the following sense (see, for example, [40])

$$me(x) \le u(t,x) \le M \quad \text{for large} \quad t > 0$$

for some $0 < m < M$ and $e(x)$ such that $e(x) > 0$ in Ω and $e(x)$ satisfies the corresponding boundary condition on $\partial\Omega$.

3. Can the restrictions on the production function be relaxed using the theory of monotone dynamical systems developed in [38, 39]?

4. For variable periodic parameters, does a positive periodic solution depend on the diffusion coefficient?

5. Consider a more general per capita production function, for example, $g(t,x)$ satisfying $g(t,x) < 0$ for $0 < x < x_0$, i.e. the models which experience Allee effect.

6. Originally some of the models described by ordinary differential equations incorporate some kind of delay (for example, the Nicholson's blowflies equation corresponding to (2.6), where the production term with exponential involves a maturation delay). Extend the results of the present paper to delay models, explore the influence of delays and compare models with two different diffusion strategies.

7. It is known that, for example, for the logistic equation with a periodic carrying capacity, the average of the positive periodic solution over the time cycle is less than the average carrying capacity [4]. Is it true for the periodic models with regular and carrying capacity driven diffusion? See Example 5 and Fig. 6 for a partial numerical confirmation of this idea.

8. Consider optimal harvesting and resources management when there are steep changes in the carrying capacity, and the optimal strategy suggested in [5] and Theorem 11 is not applicable, in particular, (7.2) is not satisfied. The difficulties of sustainable harvesting in a rapidly changing seasonal environment and relatively low growth rates are described in [37].

9. For systems with periodic parameters describe the conditions for extinction or for existence of a positive attracting periodic solution, in terms of principal eigenvalues of the linearized problem using the technique described in [38, Theorems 2.3.4, 3.1.5].

10. For which models and the values of the parameters, will the yield defined in (7.4) be also the Maximal Sustainable Yield, i.e. $u_{\max}$ be globally asymptotically stable?

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8 Appendix

Consider the following nonlinear elliptic boundary value problem

$$\begin{aligned} -Lu &= F(x,u) \text{ in } \Omega \\ \frac{\partial u}{\partial n} &= 0 \text{ on } \partial\Omega \end{aligned} \tag{8.1}$$

where the operator L defined as

$$Lu := \sum_{i,j=1}^{n} a_{ij}(t,x)\frac{\partial^2 u}{\partial x_i \partial x_j} + \sum_{i=1}^{n} b_i(t,x)\frac{\partial u}{\partial x_i} \tag{8.2}$$

is uniformly elliptic, namely, there exist positive numbers λ and Λ such that for every vector $\xi = (\xi_1, ..., \xi_n) \in \mathbb{R}^n$

$$\lambda|\xi|^2 \le \sum_{i,j=1}^{n} a_{ij}(t,x)\xi_i\xi_j \le \Lambda|\xi|^2, \;\; (t,x) \in \overline{Q}_T. \tag{8.3}$$

We assume that the coefficients of L are Hölder continuous in Q_T and the function f satisfies (A1).

The next two results are on the existence and uniqueness of the positive equilibrium [31]

Proposition 1. *[31, Theorem 3.2.2] Suppose that the function F satisfies the assumption (A1) and let $\tilde{u}$ and $\hat{u}$ be ordered upper and lower solutions of (8.1). Then problem (8.1) has a maximal solution $\overline{u}$ and a minimal solution $\underline{u}$ such that $\hat{u} \le \underline{u} \le \overline{u} \le \tilde{u}$.*

Proposition 2. *[31, Theorem 3.2.4] Let $\tilde{u}$ and $\hat{u}$ be ordered upper and lower solutions of (8.1) such that $0 < \hat{u} \le \tilde{u}$, and let $\overline{u}$ and $\underline{u}$ be the maximal and minimal solutions in $\langle \hat{u}, \tilde{u} \rangle$. Assume that the operator L has the form*

$$L = \nabla \cdot d(x)\nabla$$

and the function F satisfies (A1) in $\langle \hat{u}, \tilde{u} \rangle$. If $G(x,u) = F(x,u)/u$ is monotonically decreasing in $\langle \hat{u}, \tilde{u} \rangle$ and $F(x,u_1) = F(x,u_2)$ implies $u_1 = u_2$ then $\overline{u} = \underline{u}$ and it is the unique positive solution in $\langle \hat{u}, \tilde{u} \rangle$.

Consider a general model of the form

$$\begin{aligned} \frac{\partial u}{\partial t} &= \nabla \cdot d(x)\nabla u + \vec{b}(x) \cdot \nabla u + F(x,u) \qquad \text{in } \Omega \times (0,\infty) \\ d(x)\frac{\partial u}{\partial n} &+ \beta(x)u = 0 \qquad \text{on } \partial\Omega \times (0,\infty) \end{aligned} \tag{8.4}$$

The two following results are concerned with equilibrium solutions [10].

Proposition 3. *[10, Proposition 3.1] Suppose that*

$$F(x,u) \le g_0(x)u, \qquad \text{for } x \in \Omega$$

where $g_0(x)$ is a bounded measurable function if $\vec{b}/d$ is a gradient and $g_0(x) \in C^\alpha(\overline{\Omega})$ if $\vec{b}/d$ is not a gradient. If the principal eigenvalue σ_1 of

$$\begin{aligned} &\nabla \cdot d(x)\nabla\psi + \vec{b}(x)\cdot\nabla\psi + g_0(x)\psi = \sigma\psi \qquad \text{in } \Omega\times(0,\infty) \\ &d(x)\frac{\partial\psi}{\partial n} + \beta(x)\psi = 0 \qquad \text{on } \partial\Omega\times(0,\infty) \end{aligned} \tag{8.5}$$

is negative, then (8.4) has no positive equilibria and all nonnegative solutions decay exponentially to zero as $t\to\infty$.

Proposition 4. *[10, Proposition 3.2, 3.3] Suppose that $F(x,u) = G(x,u)u$ with $G(x,u)$ of class C^2 in u and C^α in x, and there exists $M > 0$ such that $G(x,u) < 0$ for $u > M$. If the principal eigenvalue σ_1 is positive in the problem*

$$\begin{aligned} &\nabla \cdot d(x)\nabla\psi + \vec{b}(x)\cdot\nabla\psi + G(x,0)\psi = \sigma\psi \qquad \text{in } \Omega\times(0,\infty) \\ &d(x)\frac{\partial\psi}{\partial n} + \beta(x)\psi = 0 \qquad \text{on } \partial\Omega\times(0,\infty) \end{aligned}$$

then (8.4) has a minimal positive equilibrium u^*, and all solutions to (8.4) which are initially positive on an open subset of Ω are eventually bounded below by orbits which increase toward u^* as $t\to\infty$. Moreover, if $G(x,u)$ is strictly decreasing in u for $u\ge 0$ then the minimal positive equilibrium is the only positive equilibrium for (8.4).

We will use the following property of the principal eigenvalues [10].

Proposition 5. *Denote the principal eigenvalue of (8.5) as $\sigma_1(g_0)$, then $\sigma_1(g_0)$ is increasing with respect to g_0 in the sense that if $g_0^1 \ge g_0^2$ then $\sigma_1(g_0^1)\ge\sigma_1(g_0^2)$, and if $g_0^1 > g_0^2$ on a subset of positive measure then $\sigma_1(g_0^1) > \sigma_1(g_0^2)$.*

The following two propositions deal with stability of the steady states [31].

Proposition 6. *[31, Theorem 5.4.4] Let $\hat{u}(x)$, $\tilde{u}(x)$ be ordered lower and upper solutions of (8.1) and let F be a C^1-function in $\langle\hat{u},\tilde{u}\rangle$. Then a steady-state solution u^* of (8.4) is asymptotically stable with a stability region $\langle\hat{u},\tilde{u}\rangle$ if and only if it is unique in $\langle\hat{u},\tilde{u}\rangle$.*

Proposition 7. *[31, Theorem 5.3.3] Let $u(t,x)$ be the solution of (8.4) and $u^*(x)$ be the steady-state of the same problem. If $\lambda_1 < 0$, then there exist positive numbers ρ and $\alpha < |\lambda_1|$ such that*

$$|u(t,x) - u^*(x)| \le \rho e^{-\alpha t}\psi(x) \tag{8.6}$$

whenever this inequality holds at time $t = 0$. Here λ_1 and $\psi(x)$ are the principal eigenvalue and the principal eigenfunction of

$$\begin{aligned} &\nabla \cdot d(x)\nabla\psi + \vec{b}(x)\cdot\nabla\psi + F_u(x,u^*)\psi = \lambda\psi \qquad \text{in } \Omega\times(0,\infty) \\ &d(x)\frac{\partial\psi}{\partial n} + \beta(x)\psi = 0 \qquad \text{on } \partial\Omega\times(0,\infty) \end{aligned}$$

For problems with periodic in t parameters we will apply the global attractivity result [41] for the following problem:

$$\frac{\partial u}{\partial t} - Lu = F(t,x,u), \quad (t,x) \in Q, \tag{8.7}$$

$$\frac{\partial u}{\partial n} = 0, \ (t,x) \in \partial Q, \tag{8.8}$$

$$u(0,x) = u_0(x), \ x \in \Omega. \tag{8.9}$$

Here $Q = (0,\infty) \times \Omega$, $\partial Q = (0,\infty) \times \partial\Omega$, the function $f(t,x,u)$ is periodic in t with a period T_0. Then the following result holds [41].

Proposition 8. *[41] Let $\tilde{u} \geq \hat{u}$ be a pair of constant upper and lower solutions of (8.7),(8.8) and let the function $f(t,x,u)$ be Hölder continuous in (t,x), T_0-periodic in t and continuously differentiable in u for $u \in [\hat{u},\tilde{u}]$. Then there exists a pair of T_0-periodic solutions $\overline{u}$ and $\underline{u}$ of (8.7),(8.8) with $\hat{u} \leq \underline{u} \leq \overline{u} \leq \tilde{u}$. Moreover, for any initial function $u_0(x)$ satisfying $\hat{u} \leq u_0(x) \leq \tilde{u}$ in Ω, the corresponding solution $u(x,t)$ of (8.7)-(8.9) satisfies*

$$\underline{u}(t,x) \leq \liminf_{t\to\infty} u(t,x) \leq \limsup_{t\to\infty} u(t,x) \leq \overline{u}(t,x), \quad \textit{for any} \ \ x \in \overline{\Omega}.$$

Further, if $\underline{u} = \overline{u} \equiv u^*$, then u^* is the unique T_0-periodic solution in $\langle \hat{u}, \tilde{u} \rangle$ which satisfies

$$\lim_{t\to\infty} |u(t,x) - u^*(t,x)| = 0, \quad \forall x \in \overline{\Omega}.$$

The proof of a more general result can be found in [41] (Theorem 3.2).